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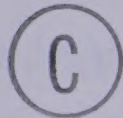
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Studies on the Heat of Warming Food in Ruminants

by



A.M. Nicol

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Doctor of Philosophy

IN

Animal Physiology

Department of Animal Science

EDMONTON, ALBERTA

Fall 1980

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled **Studies on the Heat of Warming Food in Ruminants** submitted by A.M. Nicol in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Animal Physiology.

Abstract

As ambient temperature changes, the temperature of the food and water consumed by animals also changes. The heat required to raise the temperature of ingested food and water to body temperature has generally been neglected in discussions of heat exchange in domestic animals.

A series of experiments were made to study the physiological and metabolic consequences to sheep and cattle of the heat required to warm ingested food. Rumen cooling either by an intra-ruminal cooling coil or by a ruminal water infusion was used in a number of experiments to simulate the cooling associated with the consumption of high moisture foods. Several levels and rates of rumen cooling were compared in both sheep and cattle while in a number of physiological conditions and exposed to a range of ambient temperatures.

In general rumen cooling reduced the total body heat content of the animal (mean body temperature declined); reduced the rate of heat loss from the animal to the environment (extremity skin temperature declined); and in most cases increased the rate of heat production (oxygen consumption was elevated). When pre-cooling body temperatures were high, the decline in body heat content was greater and the increase in heat production less than when lower pre-cooling body temperatures existed. The increase

in heat production in response to rumen cooling was equivalent of up to 80% of the rumen cooling imposed.

Eighty to ninety percent of the warming of the food was in the rumen in studies with cattle eating cold (2°C) and frozen (-8°C) turnips of 12% dry matter content. Also any increase in heat production in response to the requirement for heat of warming the food was temporary over the eating period and one to two hours after and was not manifest in an elevated resting metabolic rate.

Energy retention in lambs was reduced by high levels of the heat of warming, particularly at low feed intake (maintenance and below) and the reduction was dependent on ambient temperature. Dry matter or energy digestibility was not affected by the consumption of simulated high moisture feeds at low temperatures.

The heat of warming food was incorporated into a conventional body heat loss model by taking the heat flow from the body into the rumen in response to the consumption of cold feeds as a heat loss to the animal. The efficiency with which body heat could be utilised for meeting the requirements of the heat of warming food was 50 to 70%.

It was concluded that the heat of warming ingested food and water should be incorporated into heat loss models to encompass practical farming situations where the heat of warming may be an important component in the thermal balance of domestic livestock.

Acknowledgements

This study would not have been completed without:

- the continual support, help and ideas of my supervisor, Dr B.A. Young, Professor of Animal Physiology, Department of Animal Science, University of Alberta
- the facilities of the Department of Animal Science, University of Alberta, made freely available by the Chairman, Dr R.T. Berg
- the award of Study Leave by the Principal, Professor J.D. Stewart and the Council of Lincoln College, University College of Agriculture, New Zealand
- the support of Professor I.E. Coop and Professor A.R. Sykes, past and present Head of the Department of Animal Science, Lincoln College and my colleagues in the Department for shouldering additional responsibilities during my absence
- the statistical advice of Dr R.T. Hardin, Professor of Poultry Genetics, Department of Animal Science, University of Alberta and the data handling assistance of Mr R. Weingardt, Programmer with the Department
- the technical assistance of the Staff of the Metabolic Unit, University of Alberta Farm
- the camaraderie and fruitful discussions of my fellow Graduate Students and Research Associates in the

Department of Animal Science, University of Alberta
-and last but not least, the understanding and love of my
wife, Jenny

For all of the above I am deeply appreciative.

The study was financially supported in part by grants
from the Natural Science and Engineering Research Council of
Canada and the Agricultural Research Council of Alberta. A
travel grant from the Combined Beef Breeders' Research
Committee Inc., New Zealand is also acknowledged.

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Abbreviations and Terms Used

C	the rate of convective heat exchange between an animal and the environment (W.m^{-2})
Ct	total body thermal conductance ($\text{W.m}^{-2}.\text{°C}^{-1}$), the rate at which heat is conducted between the body and the environment
DE	digestible energy, equal to the combustible energy of the food eaten minus the combustible energy in the faeces
ERC	effective rumen cooling, the heat flow from the body into the rumen in response to lowered rumen temperature calculated from rumen temperature change and rumen volume and either expressed as a total quantity of heat or a rate of heat flow
G	the rate of heat exchange associated with the consumption of food and water at a temperature different from body temperature (W.m^{-2})
H	the rate of heat loss from an animal to the the environment (W.m^{-2})
HW	the total heat exchange associated with equating the temperature of food and water consumed with body temperature (kJ or MJ.meal^{-1})
IE	intake energy, combustible energy consumed by an animal ($\text{kJ.kg LW}^{-0.75}.\text{day}^{-1}$)
K	the rate of conductive heat exchange of an animal with the environment
LW	liveweight of an animal (kg)
M	the rate of heat gained by an animal from chemical energy transformations in the body expressed in physiological terms as W.m^{-2} and in nutritional terms as $\text{kJ.kg LW}^{-0.75}.\text{day}^{-1}$. M is commonly called heat production of an animal
M*	heat production in thermoneutrality i.e. when the environment has no direct influence on the rate of heat production
ME	metabolisable energy, equal to digestible energy minus energy losses from the body in

urine and combustible gasses of digestion

- R the rate of radiant heat exchange of an animal with the environment
- RE retained energy, being the difference between M and ME
- S the rate of heat storage in the body (W)
- T temperature ($^{\circ}\text{C}$) followed by an italicised letter or word to denote specific temperatures
e.g. T_a = ambient temperature
- T_c critical temperature, the ambient temperature below which no further decrease in body heat loss occurs
- W watt, $1 \text{ joule} \cdot \text{second}^{-1}$

1. INTRODUCTION

Improvement in the productivity of domestic livestock is made through good managerial decisions based on sound nutritional, genetic and physiological principles.

As animals of superior genetic merit are bred and more well defined nutritional regimes are developed, the interaction of the animal with its environment must be more clearly understood if maximum improvement in productivity is to be attained.

Considerable study in the field of environmental physiology has been made, particularly with regard to both long and short-term responses of animals to a change in ambient temperature. As ambient temperature changes, the temperature of the food and water consumed by an animal also changes. Little attention has been paid to the effect of food and water temperature on domestic livestock.

The aim of this study was to investigate some of the physiological and metabolic responses of sheep and cattle to the consumption of food of various temperatures, to evaluate the importance of the temperature of the food in influencing animal productivity and to integrate the heat of warming food into present models of the thermal balance of livestock.

2. BACKGROUND REVIEW

Domestic animals are physical systems and as such must obey the laws of thermodynamics. The first law, the conservation of energy, demands that any net change in the energy gained or lost by a system must be balanced by an equal change in the energy stored in the system.

2.1 Energy Balance

Two forms of energy, chemical and thermal, are of major importance in the living animal.

Chemical energy, in the biological context, is the free energy change associated with the oxidation of organic compounds to carbon dioxide. Chemical energy balance of the body is expressed as the following function equating retained energy (RE) with energy gain (EG) and energy loss (EL).

$$RE = EG - EL \dots\dots\dots(1)$$

Chemical energy gain by an animal is through food intake, and chemical energy is lost from the body in faeces, urine and the gaseous products of digestion.

Thermal energy (heat) balance in an animal is conventionally expressed as

$$S = M - H \dots\dots\dots(2)$$

where S is the rate of heat storage, M is the rate of heat

gained by the animal as a result of chemical energy transformations within the body, commonly called heat production or metabolic heat and H is the net rate of heat loss from the animal to the environment. Metabolic heat (M) can be indirectly estimated from empirical equations relating the oxidation of carbohydrate, fat and protein to a calorific value for the gaseous exchange of the animal (Brouwer, 1965; McLean, 1972). This form of indirect calorimetry is widely used in estimating M in animals.

The net rate of heat loss (H) can be measured using direct calorimetry; a procedure which is not widely used due to the cost and technical difficulties involved. With domestic livestock, more emphasis has been placed on measuring individual components of overall heat exchange and predicting these from physical characteristics of the animal and the environment (Blaxter et al., 1958a; Blaxter and Wainman, 1961; Joyce and Blaxter, 1965; Webster, 1971; Mount, 1977).

Heat exchange between the animal and the environment is normally expressed as a function of the following rates of heat exchange

$$H = E + R + C + K \dots\dots\dots (3)$$

where E , R , C and K are the rates of heat exchange with the environment by evaporation, radiation, convection and conduction respectively. Heat exchange due to R , C and K are often termed sensible or Newtonian heat exchanges.

The above thermal balance equation (3) has been

presented in many recent reviews on environmental physiology (Alexander, 1974; Ingram, 1974; Mitchell, 1974; Webster, 1974). This equation neglects a further source of heat exchange through the food and water ingested by the animal. Furthermore, Bligh and Johnson (1973) in their glossary of preferred thermal physiological terms do not acknowledge the contribution of ingested food and water to thermal balance of animals.

The consumption of food and water is associated with a gain of mass and heat to the body. If the temperature of the food and water is below body temperature, then the relative gain in heat will be less than the gain in mass and mean body temperature should fall. The quantity of heat required to raise the temperature of the mass of the ingested food or water to body temperature has conventionally been referred to as the *Heat of Warming*, either expressed as an absolute quantity of heat (HW) or as a rate (G) per unit time.

The term *heat of warming* will be used throughout this study although it is somewhat of a misnomer. Except for special cases such as the Scotsman with his bowl of hot porridge, the heat of warming represents a net *cooling* of the body when food or water is consumed at temperatures below body temperature. HW is normally calculated as the product of the difference between the temperature of the body (T_b) and food or water (T_i), the mass of the food or water ingested (W_i) and the specific heat of the food and

water (Sh_i).

$$HW = (T_b - T_i) \times W_i \times Sh_i \dots\dots\dots(4)$$

Where a change from solid to liquid phase is involved in the heat of warming, as when snow or frozen food is ingested, the latent heat of fusion must also be included in the equation.

Although heat is also lost when an animal defaecates and urinates, this heat loss is associated with a loss in mass at body temperature and is not considered as a net loss of heat to the animal (Blaxter et al., 1958b) although it is measured as such in direct calorimetry (Watts et al., 1977).

Evaporative (E) heat exchange is also associated with a change in mass of an animal, but the mass change is small relative to the change in heat with the change in phase of the water. Newtonian heat exchanges are not associated with concomitant changes in body mass.

2.1.1 The Magnitude of the Heat of Warming

The absence of HW from many published thermal balance equations may be because HW is considered to be of little consequence in the overall thermal balance of domestic animals or because the waste heat of digestion and energy utilisation is more than sufficient to cover HW (eg. Butcher, 1973). Blaxter (1962) calculated that HW for sheep and cattle fed dry rations was equivalent to 2 to 4 $W.m^{-2}$ or less than 4% of total daily heat loss. On high dry matter rations HW does not increase to any appreciable extent as

ambient temperature (T_a) decreases, at least to 0°C because drinking water intake tends to decline as T_a falls.

There are however, practical farming conditions where calculations suggest that HW could be an important component in the thermal balance equation. Blaxter (1962) calculates that under winter conditions (T_a approximately 7°C), where animals are consuming high intakes of bulky high moisture feeds such as root crops or silage, HW could be equivalent to 14% of total daily heat loss. A similar calculation by Barry et al. (1971) for young sheep with a known voluntary intake of high moisture content crops, indicated that HW was equal to 6 to 15% of daily digestible energy intake.

When animals consume snow or ice either involuntarily during grazing, or as the only source of water, HW may be large due to the latent heat of fusion. Young et al. (1979) have calculated that where beef cows have snow as the only source of water, HW would theoretically be equal to 15 to 20% of digestible energy intake.

Unlike sensible and evaporative heat exchanges which are continuous, eating and drinking occur sporadically during the day. For example, if a 400 kg steer consumed 15 kg of turnips at a temperature of 2°C in one hour, HW would be 1.96 MJ or 110 W.m^{-2} which would be the equivalent of approximately 70% of the heat production of a well-fed steer over the hour of eating. Although HW is small when expressed as a % of daily H, its real impact on thermal balance may be greater over the shorter term.

Newtonian and evaporative heat exchanges are functions of the environment and the insulation and metabolic rate (M) of the animal. The animal thus has some control over the rate of heat exchange through changes in posture, thermal insulation, peripheral blood flow, rate of sweating and panting, shelter seeking behaviour, etc. On the other hand HW is a function of the environment and the food and water consumed so that the animal has less control over HW other than by changes in quantity or pattern of food and water intake.

2.1.2 Heat Storage

No continuous increase or decrease in T_b is compatible with sustained homeostasis. Thus long term change in heat storage can only be associated with a change in body mass. However homeotherms do exhibit short term (minutes to days) fluctuations in mean body temperature (T_b) which indicate variation in S when mass and specific heat remain constant. As Bligh (1973) has emphasised, the difference between homeotherms and poikilotherms is more a matter of degree than fundamental principle. Change in the rate of heat storage is likely to play a role in thermal balance in the short term. Change in S and total body heat content (HC) can be estimated in a number of ways. Heat storage can be measured as the difference between M measured by indirect calorimetry and H , either measured by direct calorimetry or taken as the summation of E , R , C and K heat exchanges

measured or predicted.

In an exercising man S can reach 100 W over the first few minutes of exercise (Chappuis et al., 1976) or be maintained at -20 to -40 W for a continuous period of 2 h under mild cold exposure. As a result of such changes in S , total body heat content (HC) in man can rise 100 kJ with exercise (Chappuis et al., 1976), 550 kJ with heat exposure (Horstman and Horvath, 1972) or decline by 750 kJ with mild cold exposure without the onset of shivering (Hardy and Stolwijk, 1966). Watts et al. (1977) have shown normal daily fluctuations in the HC of calves of 600 kJ, from a low of -200 kJ below mean daily HC prior to feeding in the morning to +400 kJ after afternoon feeding. S was estimated to be 10 to 12 W for the first 4 h post-feeding.

An alternative approach to estimating changes in body heat storage is to calculate body heat content repeatedly over time. Body heat content (HC) is the product of the heat capacity of the body (mass \times specific heat) and the mean temperature of the body tissues (see Minard, 1970). From changes in mean body temperature (T_b), Blaxter et al. (1958a) calculated a change in HC of 1.3 MJ in sheep over a range of ambient temperatures from 10 to 50°C. Standing has been shown to reduce HC of sheep by 33 kJ (Brockway, 1965).

Mitchell (1977) reiterated the concern of many authors about the accuracy of assessing T_b from weighted combinations of various body and skin temperatures. This

concern is particularly relevant in short-term, non-steady states where thermal gradients within the body have been disrupted. Although of limited accuracy, thermometry continues to be used to estimate relative changes in S with time. Changes in T_b have been shown to occur in domestic livestock and man with heat and cold stress (see review by Thompson, 1973), with shearing (Bailey, 1964; Webster, 1966), with eating (Ingram and Whittow, 1962) and with the consumption of cool milk (Holmes, 1971b) or ice-cream (Nadel et al., 1970).

2.2 Physiological and metabolic consequences to domestic livestock of the Heat of Warming

The scientific literature contains many reports on the physiological effects of varying the temperature of drinking water or liquid diets. Although in many of these reports the heat of warming *per se* was a side issue in the experiment, these experiments do form a useful data base.

The following parameters have been shown to be influenced by HW in domestic livestock.

2.2.1 Rumen temperature

When water is consumed or poured into the rumen at temperatures below body temperature, rumen temperature declines (Bailey, 1964; Bhattacharya and Warner, 1968; Butcher, 1973; Cunningham et al., 1964; Dale et al., 1954; Dillon and Nicholls, 1955; Nangeroni, 1954; Noffsinger et

al., 1961; Webster and Johnson, 1968). The extent of the drop in rumen temperature (Tru) is influenced by the quantity and temperature of the water and can be as great as 15°C . The recovery in Tru is quite rapid with about 50% of the recovery occurring in 15 to 30 minutes (Watts et al., 1977). Nangeroni (1954) reported that sheep eating cool (no temperature stated) fresh alfalfa showed a drop in rumen temperature which more than negated the rise of 0.8 to 1.3°C which occurred after eating dry rations.

Thermal receptors are present in the rumen wall (Rawson and Quick, 1972). Thus responses to rumen cooling could be via such receptors and need not depend on stimulation of deep body thermal receptors. Cold food and water ingested through the mouth presumably reduce the temperature of tissues of the mouth. Thermal receptors have been identified in the mouth of the cat (Bligh, 1973) but no attempt seems to have been made to measure changes in mouth temperature of ruminants during the ingestion of cold food or water.

2.2.2 Skin Temperature

A large decline (12°C) in ear skin temperature ($Tear$) due to peripheral vaso-constriction occurred in sheep given 500 ml of iced water intra-uminally (Webster and Johnson, 1968). The skin temperature of calves and pigs fed cold milk or whey fell significantly when Ta was warm (25°C) but not at cool (15°C) ambient temperatures (Holmes, 1970;

1971b). At a low T_a (-12°C), the subcutaneous tissue temperature of sheep tended to be higher when the temperature of the drinking water was reduced (Bailey, 1964).

The decline in skin temperature with ruminal cooling seems to be dependent on T_a . In a behaviour study with operantly conditioned sheep, Baldwin (1975) was able to show that as ambient temperature declined, ruminally cooled sheep used an infra-red heater for a longer period of time. The sensation of internal cooling was not reduced at the lower ambient temperatures. At lower T_a , peripheral vaso-constriction caused by the T_a per se, reduced the potential for a further drop in skin temperature with ruminal cooling. Since peripheral vaso-constriction is caused by sympathetic nerves and the neurotransmitter at the post-ganglionic neuron to smooth muscle junction is norepinephrine (NE) (see Thompson, 1977 review) an elevation in circulatory NE level might be expected in response to rumen cooling. Illner et al. (1977) have shown a doubling of serum NE levels in goats subjected to ruminal cooling and high levels were maintained for 1 to 2 h after cooling.

2.2.3 Respiratory Frequency

Respiratory frequency has been observed to fall by 50% with gastro-intestinal cooling in pigs (Holmes, 1970) and sheep (Webster and Johnson, 1968; Rawson and Quick, 1972) and to remain depressed for 70 to 150 min post-cooling.

Reduced evaporative heat exchange is a documented response to ambient cooling and contributes to the reduction in heat loss within the thermoneutral zone.

2.2.4 Deep Body Temperature

The rectal temperature (40.2°C) of heat stressed cattle can be reduced by rumen cooling (Bianca, 1964). Rectal temperature has been shown to fall by up to 1.9°C in pigs and 1.1°C in calves consuming cold liquid food (Holmes, 1970, 1971a). A decline in rectal temperature (T_r) with rumen cooling has also been demonstrated in sheep (Noffsinger et al., 1961; Rawson and Quick, 1972) and in goats (Illner et al., 1977). However Bailey (1964) and Webster and Johnson (1968) did not find a decline in T_r as rumen temperature dropped.

Rectal temperature is only one of a number of deep body temperatures which can be measured. Rawson and Quick (1972) measured small decreases in hypothalamic temperature with rumen cooling but a larger drop in the temperature of the vena cava of up to 1°C . Vagina temperature declined to a similar extent. The decline in carotid artery temperature can be greater (by $0.2\text{--}0.8^{\circ}\text{C}$) than the fall in rectal temperature with stomach cooling (Holmes, 1970). The latter illustrates the relative thermal inertia of rectal temperature.

A decline in deep body temperatures can occur with stomach cooling but a decline is not inevitable. A decline

in rectal temperature seems to depend on the extent of the cooling.

2.2.5 Shivering

Shivering has been recorded in calves drinking cool milk (Holmes, 1971b), in pigs consuming cool whey (Holmes, 1970) and in sheep and goats with artificially cooled rumens (Rawson and Quick, 1972; Illner et al., 1977). Shivering occurred on fewer occasions in pigs and young calves fed cool whey and milk when T_a was higher (Holmes, 1970, 1971a). In other cases, shivering was not observed with stomach cooling (Bailey, 1964; Webster and Johnson, 1968). When men rapidly consumed 500 g ice-cream at a T_a of 10°C they shivered, but at 44°C the response to ice-cream consumption was restricted to reduced peripheral heat loss (Nadel et al., 1970). The decision as to whether an animal is shivering or not is usually subjective. As Webster (1974) has emphasised, the absence of overt shivering does not necessarily mean that striated muscles are not responding to the stress of cold by increases in muscle tone or minor tremor.

2.2.6 Metabolic Rate

Metabolic rate (M) increased 80% in sheep undergoing an unspecified amount of rumen cooling (Rawson and Quick, 1972). The increase in M was not dramatic until core temperature had declined by 0.75°C. The oxygen consumption

of calves effectively cooled by 250 kJ by consuming cool milk (23°C) was elevated during milk consumption by a maximum of 30% above that of calves drinking warm milk (39°C). The cumulative increase in \dot{M} accounted for 79% of the calculated HW (Holmes, 1971a). These increases in \dot{M} were associated with shivering. Luick (1976) states that "the energy cost of warming snow (and frozen vegetation) increases the resting metabolic rate of reindeer by approximately 35%".

Acute exposure to high levels of HW can cause a temporary rise in \dot{M} , but no long-term studies have been made to determine if a rise in resting metabolic rate would result from repeated cooling by HW. Sheep and cattle exposed to low ambient temperatures for extended periods of time have shown an elevation in metabolic rate (Webster et al., 1969; Young, 1975).

2.2.7 Feed Intake

Supplying drinking water at 18 to 20°C in a hot (>35°C) environment increased food intake of cattle (Ittner et al., 1951; Lofgreen et al., 1975). Since food intake is depressed by high T_a (see Thompson, 1973), the cooling effect of the water maintained at the lower temperature apparently restored the higher food intake. Lofgreen et al. (1975) using the equations of the Californian Net Energy system calculated that the HW of the cool water was almost exactly equal to the increment in \dot{M} predicted from the measured

increase in food intake.

At thermoneutral T_a , dairy heifers regularly cooled with ruminal infusions of cold water for 7 h, increased their intake of a *dry* food (Bhattacharya and Warner, 1968). Prolonged low ambient temperatures increase voluntary food intake (Thompson, 1973). On the other hand, calves fed cold milk while grazing showed a decline in milk intake compared with calves fed warm milk (Tayler and Lonsdale, 1969). Water intake declines with ambient cooling (see Bianca, 1965). With high moisture feeds, where the feed supplies more than sufficient water for normal body function, a paradox exists between a potential rise in food intake but a decline in water intake as T_a falls.

2.2.8 Digestibility and Rumen Fermentation

Although energy and nitrogen digestibility have been shown to decrease as T_a falls (Christopherson, 1976), there is little evidence that a decline in food digestibility occurs with increasing HW (Cunningham et al., 1964; Sims and Butcher, 1973; Brod, 1979). When rumen temperature was raised artificially to 43°C an increase in volatile fatty acid (VFA) concentration occurred, but with a further increase to 51°C VFA concentration fell by 50% (Gengler et al., 1970). Brod (1979) measured lower concentration of VFAs in the rumen fluid of sheep loaded intra-uminally with 2 litres of cold water after eating. Temperature is one of the most important variables affecting the growth of

micro-organisms (Clarke, 1977), but reduced VFA concentrations may not necessarily be indicative of reduced total fermentation since a slower rate of fermentation may be maintained for a longer time. Even if ruminal fermentation was depressed with continued ingestion of cold feed, compensatory digestion in the post-ruminal digestive tract, as has been shown to occur with prolonged low ambient temperatures (Kennedy et al., 1976), might result in no important change in overall digestibility.

2.2.9 Liveweight Gain and Feed Conversion Efficiency

At high ambient temperatures, a supply of cool water increased the liveweight gain and food conversion efficiency (FCE) of cattle (Ittner et al., 1958; Lofgreen et al., 1975). When sheep consumed snow as their only source of water their liveweight gain was no lower than sheep with drinking water (Butcher, 1973) but calves drinking cold milk grew 12% more slowly partly due to a reduction in milk intake (Tayler and Lonsdale, 1969). Pigs fed cool (15°C) whey gained weight more slowly (5 to 11%) and FCE was significantly poorer than in pigs fed whey at 40°C. The dry matter of the whey was 6%. But when a gruel of meal and water (2.5:1) was fed at three temperatures (5, 13, or 35°C) to pigs, no difference in the rate of gain was observed. (Forbes and Walker, 1969)

On the basis of a review of field experiments in New Zealand on the growth rate of young sheep and cattle grazing

high moisture crops during winter, Nicol and Barry (1980) speculated on a possible reduction in liveweight gain as a result of the high HW of these rations. By comparing actual liveweight gain with gains predicted from known feed intakes and the ARC (1965) feeding standards, the authors estimated that on average, 70% of the difference between actual and predicted gain could be accounted for by the theoretical calculation of the HW.

2.3 Overview and Objectives of the Study

There have been few research studies designed specifically to investigate the physiological and metabolic consequences to animals of ingesting cold feeds and water. This is no doubt a reflection of theoretical calculations which indicate that under most situations the heat required to warm ingested food and water to body temperature is small in relation to the total heat loss of the animal. However, there are situations where HW can be large and may have important practical consequences. For example, it has been estimated that high moisture feeds (<15% dry matter) grazed over the winter in New Zealand provide 10^9 sheep grazing days (Nicol and Barry, 1980). Thus even a small reduction in productivity per animal due to high HW could have a large total cost to the industry. Furthermore many beef cows and much of the wild-life in the colder areas of North America may have access only to snow as a source of water for many months.

Only the work of Holmes (1970, 1971a,b) has been designed specifically to study the practical production effects of heat of warming (HW) and these experiments were on pigs and calves which are, in thermal terms, unstable animals compared to sheep and older cattle. Much of the work reviewed in the previous section has not had the effects of HW as the prime objective of the study, but in many respects the physiological and metabolic responses of animals to HW seem to be similar in type, if not quantitatively, to those induced by a change in ambient temperature. However, there has been little work on the inter-relationships of the physiological and metabolic responses to HW with the absolute quantity (HW) and rate (G) of the heat of warming.

There is some evidence that the effects of HW are dependent on environmental temperature but no indication as to whether the time of cooling, relative to eating is important. Furthermore, the effect of cooling per se, independent of the associated mass or water load has not been established. The physiological state of the animal in terms of feed intake or natural insulation may be expected to affect the response to HW.

Temporary changes in the rate of heat storage (S) may be involved in regulating the effects of HW, but there is no evidence to what extent S may change with various levels of HW.

There is evidence that the liveweight gain of animals

can be depressed when HW is high but that the depression is not as great as theoretical calculations would suggest. The reasons for this discrepancy are speculative.

It is not currently possible to make many definitive statements on the importance of HW in practical animal husbandry situations.

The objectives of this study were threefold-

1. To examine inter-relationships which may exist between the heat of warming food (HW) and the physiological and metabolic responses of sheep and cattle to HW.
2. To measure the influence of varying levels of HW on energy retention and changes in M and H.
3. To consolidate the results of the above into a model to assist in predicting the likely importance of HW in practical farming situations.

3. GENERAL METHODS

Many of the facilities, equipment and techniques used in the study were common to all experiments. Where variation from these common methods arise, further description is given under the individual experiment. Eleven experiments were conducted but they have been grouped together for presentation on the basis of their objectives and design.

3.1 Location

The complete study was made in the Metabolic Unit of the University of Alberta Farm from May 1978 to December 1979. Except where specified the experiments were all made in the same continuously lighted room maintained at an air temperature of $10 \pm 2^{\circ}\text{C}$. Air movement at animal height in the room was approximately $0.2 \text{ m}\cdot\text{sec}^{-1}$.

3.2 Animals and Feeds

All animals were selected from those bred on the Farm or the University Ranch. During experiments animals were kept in metabolism crates. The sheep crates had an expanded metal plate floor ($1.8 \times 0.4 \text{ m}$) raised 0.75 m from the ground. The sides and back of the crate were moulded fibreglass panels. Feed and water containers were positioned at the front of the crate. To prevent the sheep from chewing

equipment attached to them they were tethered by a collar and 0.5 m of light chain to the floor of the crate. Cattle crates had a floor area of 3x1 m which was raised 0.3 m from the floor. Cattle were held in neck yokes and fed in wooden boxes at the front of the crate. Four feeds were used during the experiments (Table 3.1).

Table 3.1 Description of feeds used in the experiments

Feed	Description	Dry matter (%)	Crude protein (%)	Experiment
Ration A	Concentrate	86.0	16.8	I, II, III, IV VIII, IX, XI
Turnips	Turnip bulbs	12.5-13.0	8.9	V, VI, VII, X
Long hay	Brome grass mixture	88.5	7.4	IV
Chopped hay	Brome grass	86.4	8.8	V, VII, X

The concentrate ration (Ration A) was 50% barley, 50% alfalfa meal with appropriate mineral and vitamin supplementation and was pelleted through a 4 mm die.

3.3 Respiratory Gaseous Exchange

Oxygen consumption, carbon dioxide and methane production were measured using a ventilated hood and the open-circuit indirect calorimetry system described by Young et al. (1975). Two calorimeters were used, System A and System B.

With system A baseline (atmospheric air) and standard gas calibrations (17 to 18% oxygen, 2% carbon dioxide and 0.3% methane) were made at the beginning and end of each trial, or at 8 h intervals during 24 h measurements.

In system B, with which only oxygen consumption was measured, a two channel paramagnetic oxygen analyser (Taylor Servomex Model OA184 and ratio box 228) substituted for the Beckman Model F3M analyser used in system A. System B was calibrated with atmospheric air and nitrogen gas on the full scale setting (25 cm chart width) of 25% oxygen on the ratio box. Measurements were made with a full scale setting of 1 or 2.5% oxygen in the differential mode which monitored the difference in oxygen content of the air entering and leaving the ventilated hood.

Respiratory gaseous exchange was calculated over 10 to 30 minute periods from the strip-chart recording of the continuous change in % oxygen, carbon dioxide and methane content of air drawn from the hood. Where oxygen, carbon dioxide and methane were measured, metabolic heat production (M) was calculated using the equation recommended by Brouwer (1965)

$$M = 16.18O_2 + 5.02CO_2 - 2.17CH_4 - 5.99N \dots (5)$$

where M is heat production (kJ) and O_2 represents the volume (litres, STP dry) of oxygen consumed, CO_2 is the volume of carbon dioxide produced, CH_4 the volume of methane produced and N the nitrogen (g) excreted in the urine over the balance period. When only oxygen consumption was measured,

the simplified equation of McLean (1972) was used to calculate heat production, where $M \text{ (kJ)} = 20.44 \times \text{the volume (litres, STP dry) of oxygen consumed.}$

The ventilated hoods were of sealed 12 mm plywood. The removable front which contained an area of plexiglass sealed with caulking compound was held, sealed with weather stripping to the hood with spring clips. A plastic webbing material drawn snugly round the neck of the animal enclosed the head of the animal in the hood. The volume of the cattle hood was 900 litres and the sheep hood 200 litres. Flow rates (STP, dry) through the hoods were 30 to 60 litres.min⁻¹ for sheep and 290 to 300 litres.min⁻¹ for cattle.

3.4 Body Temperature Measurements

Body temperatures were measured with copper-constantan thermocouples connected to a 24 channel millivolt recorder (Honeywell Controls Ltd., Model Electronic 15) with a full scale of +50 to -50°C and an internal reference milli-voltage. When fewer than 24 thermocouples were in use two to three channels were wired in series to record the output from one thermocouple. The recorder printed one channel per 15 sec.

All thermocouple junctions were soldered and two types of thermocouple wire were used. Type A, 36 swg zip cord and Type B, 28 swg PVC sheathed, (both from Thermo-electric Ltd., Brantford, Ontario). The following temperatures were

measured.

3.4.1 Rectal Temperature

To measure rectal temperature (T_r) a type B thermocouple was taped to the end of a 10 cm rectal probe and held in place by tying to the fleece (sheep) or to the sides of the crate (cattle) with flexible ties.

3.4.2 Skin temperatures

Ear skin temperature (T_{ear}) was measured on the clipped surface of the distal one third of the external surface of the ear. The thermocouple (type A for sheep and B for cattle) was held to the skin by contact glue and a crossed strip of adhesive tape (25 mm wide). The leg skin thermocouple (type B) was secured to the clipped surface of the lower hind limb by a single thickness of 50 mm wide medical adhesive tape. Trunk skin temperature (T_t) was measured mid-side for sheep and on the shoulder on cattle. For sheep, type A wire was enclosed in polyethylene catheter tubing (Intamedic PE190, I.D. 1.19 mm, Clay Adams Ltd.). The end of the catheter was heated, flattened and anchored to the skin by a suture at the end and approximately 25 mm from the end. With cattle a type A thermocouple was held in place on the skin by twist ties in the hair.

3.4.3 Rumen Temperature

Type B thermocouples were inserted through the rumen

cannula and either weighted (bottom) or suspended in the rumen contents (core) to measure rumen temperature (Tru)

All body and rumen temperatures were monitored continuously during a trial and the mean value (to the nearest 0.1°C) over 10 to 30 min periods transcribed from the strip chart.

3.4.4 Mean Skin and Body Temperature

Mean skin (Tsk) and mean body temperature (Tb) were computed from the body temperatures recorded as follows

$$Tsk = 0.2 \times ((Tear + Tleg) \div 2) + 0.8 \times Tt \dots (5)$$

The weighting of extremity ($Tear$, $Tleg$) and trunk temperature was that suggested by Webster and Johnson (1968). The equation of Burton and Bassett (1936) was used to estimate mean body temperature

$$Tb = 0.33 \times Tsk + 0.67 \times Tr \dots (6)$$

3.5 Rumen Cooling Coil

Rumen cooling coils were constructed for both sheep and cattle. Lengths of thin walled PVC laboratory grade tubing of the dimensions shown in Table 3.2 were connected in parallel to a copper tubing manifold inserted through a plug of appropriate size to comfortably replace the normal rumen cannula plug.

The temperature and flow of water through the coil were regulated by a 12 mm gate valve and a mixing valve (Bradley

Table 3.2 Dimensions of rumen cooling coils for sheep and cattle

	Number of coils	Length (m)	Internal dia. (mm)	Wall thickness (mm)
Sheep	4	1.5	3.0	0.7
Cattle	2	8.0	13.5	1.5

Corp., Menomonee Falls, Wis., Model 5127J), supplied with hot and cold domestic water. Flow rate through the coil was measured by stopwatch and measuring cylinder

A thermocouple (type B) was mounted in the inlet and outlet lines 5 cm from the entry to the rumen. The temperature differential between the water entering and leaving the coil was monitored by a digital thermocouple recorder (Bailey Instruments Inc., Model BAT 8) set in the differential mode.

3.6 Statistical Analyses

All data were subjected to analysis of variance using appropriate linear models for each particular experiment. Multiple comparison of means was by a Student-Newman-Keuls test. Where interaction means were statistically significant by an F-test, they were compared by the Cicchetti approximation (Cicchetti, 1972). Where more than three consecutive 10 minute observations of a temperature in any trial were missing (usually due to the malfunction of a thermocouple junction), the mean value from other replicates

was substituted and the error degrees of freedom appropriately reduced. A least squares analysis of variance for unequal numbers was only used (Experiments IX and XI) when one complete cell of data was missing.

In general only significant results are shown in the text and the results of the complete statistical analysis are shown in the appropriate appendix. The appendix for each experiment also includes more detailed data. Raw data is stored on a computer tape (MICO), held by the Department of Animal Science, University of Alberta.

4. EXPERIMENTS I, II and III IMMEDIATE RESPONSES OF SHEEP TO THE HEAT OF WARMING

The objective of these first three experiments was to obtain some basic data on the immediate responses of sheep to the heat of warming.

The heat of warming (HW) ingested food and water is associated with a change in body mass in addition to a change in the heat status of the animal. In comparing HW with other forms of heat exchange between the animal and the environment, the relative importance of the mass and temperature components of HW should be understood.

Feeding is accompanied by a rise in heat production (M) which is a function of the physical ingestion of food (prehension, mastication, saliva secretion and gut motility) and the heat released during the catabolism of the chemical energy consumed (Webster, 1972). Drinking on the other hand is not associated with an intake of available chemical energy. The possible significance of the association of HW with either eating or drinking is not known.

The effect of HW on animals is likely to be influenced not only by the temperature of the food and water, which determines the total quantity of HW, but also by the rate at which food and water are ingested. The significance of the rate of body cooling through HW is unclear.

The response of an animal to HW may be influenced by the total heat content of the body. Body heat content is to some extent dependent on the physiological state (feed intake, external insulation etc.) of the animal. The possible interaction of HW with the physiological state of an animal needs clarification.

This group of experiments examined the immediate responses of sheep to:

1. rumen cooling by the addition of a cool mass or withdrawal of heat
2. levels of rumen cooling equivalent to the consumption of high moisture feed at temperatures from 38 to 1°C
3. rumen cooling before, during or after eating
4. various rates of rumen cooling and
5. rumen cooling of well and poorly fed and insulated sheep.

4.1 Experiment I The effects of ruminal cooling by two methods in fed and unfed sheep

Changes in body temperatures, urine output, heart rate and metabolic rate were measured in three woolly sheep in which the heat of warming was simulated by rumen cooling. The cooling was by water infused into the rumen or by a intra-ruminal cooling coil. Three levels of rumen cooling were compared and cooling was imposed during feed ingestion or before feeding.

Each trial consisted of a 1 h pre-treatment period (Period I), followed by a 1 h treatment (cooling/eating, Period II) and two 1 h recovery periods (Periods III and IV).

4.1.1 Experimental Methods

4.1.1.1 Animals

Three Suffolk cross, 1.5 year old, fully fleeced (10 to 15 cm fleece depth) wether sheep weighing 45.5 ± 1.5 kg were used in Experiments I and II. Two of the same sheep were used in Experiment III.

Surgical Preparation

All sheep had been prepared with a rumen fistula one year prior to these experiments. Two weeks prior to the experiment, four thermocouples (type A) sealed in medical grade polyethylene catheter (Intramedic PE 190, I.D. 1.19 mm, Clay Adams Ltd.) were surgically implanted to measure

specific intra- and extra-ruminal temperatures. General anaesthesia was induced with an intravenous injection of sodium thiamylal (Bio-Tal, Bio-Ceutic Laboratories Inc., Missouri) and maintained with a fluothane/oxygen mixture via an intra-tracheal tube. The rumen wall was located through a 10 cm incision on the right side of the animal 10 cm caudal to the last rib and 15 cm lateral to the spine. The flattened end of one thermocouple cover was sutured to the surface of the dorsal sac of the rumen approximately 2 cm dorsal and caudal of the right rumen vein. A second thermocouple was inserted through the rumen wall to lie inside the lumen of the rumen juxtaposed to the extra-ruminal thermocouple and was sutured in position. A similar pair of thermocouples were sutured on the ventral sac. The thermocouple wires were exteriorised through individual stab wounds dorsal to the main incision.

During the same operation two of the sheep were prepared with a supra-pubic urinary drain. The bladder was located through a 5 cm para-medial incision anterior to the scrotum. The drain (Silastic malecot catheter no. 32, American Latex Corp., Sullivan, Indiana) was inserted and secured with a purse string suture, exteriorised through a stab wound and strapped to the hind leg. These drains did not maintain patency for the complete experimental period as they became occluded with fibrous tissue. After blockage of the bladder drain, urine was collected as voided. The third sheep was not fitted with a drain, but approximately one

third of the surface area of the bladder was infolded and sutured into the body of the bladder in an attempt to restrict the volume of the bladder and induce more frequent urination.

4.1.1.2 Experimental treatments

The following treatments were incorporated in a 3x2x3x2 randomised split-plot design using three sheep, two methods of rumen cooling, three levels of rumen cooling and rumen cooling with or without associated feeding. Each sheep was subjected to the complete series of 12 trials allocated randomly over a continuous 12 day period. One trial per day was made on each sheep.

Method of Rumen Cooling Treatments

1. INFUSION

Water was infused into the rumen via the rumen cannula at a rate of 2.5 litres.h⁻¹ over Period II. This quantity of water represents a dry matter:water intake ratio of 1:10 when food was ingested (see FED treatment). The water was infused by a peristaltic pump (Cole Palmer Instrument Co., Model Masterflex 7545) and the rate checked by stopwatch and measuring cylinder.

The temperature of the infusate was monitored by a thermocouple placed in the insulated delivery tube approximately 5 cm from the entry to the rumen. The

infusate was stored in a thermostatically controlled water bath and passed through an insulated water:polyethylene glycol circulated catheter cover (Hills et al., 1977) before entering the rumen.

2. COIL

The sheep rumen cooling coil was inserted into the rumen through the cannula at the beginning of Period II and removed after one hour. The flow rate and temperature of the water entering the coil were adjusted to give the appropriate temperature differential across the coil calculated to withdraw the required quantity of heat from the rumen. Flow rate through the coil was between 1 and 2.5 litres.min⁻¹. In-going temperature of the circulating water was 22 to 25°C and the temperature differential across the coil 2 to 3°C.

Level of Rumen Cooling Treatments

1. NIL

During Period II, water (2.5 litres) was infused intra-uminally at 39°C (INFUSION) or the cooling coil was in place but with no circulation of coolant (COIL). There was no net cooling of the animal with this treatment.

2. LOW

A total of 210 kJ of ruminal cooling over the 1 h treatment period. This level of cooling was equivalent to consumption of a ration of 10% dry

matter at 19°C and represented a rate of rumen cooling of 58 W.

3. HIGH

A total of 400 kJ of ruminal cooling over the 1 h treatment period. This was a rumen cooling rate of 116 W and was equivalent to the consumption of a ration of 10% dry matter at 1°C.

Fed - Not Fed Treatment

1. FED

A total of 250 g Ration A was fed in 6 equal portions over the one hour treatment period (Period II). This rate of eating was 4 to 5 g dry matter.min⁻¹, equivalent to that reported for high moisture feeds (Graham, 1964a; Osuji, 1974).

2. NOT FED

No feed during the trial.

In each case, the balance of the daily ration of 1000g Ration A was fed at the conclusion of each trial. When not on test the sheep were fed the full daily ration at 0900 h.

4.1.1.3 Measurements and statistical analysis

Continuous recordings of oxygen consumption, ear and leg skin temperatures, rectal temperature and five rumen

temperatures (four thermocouples surgically attached to the rumen wall and one inserted through the cannula into the rumen core) were made over the four hour trial. Trunk skin temperature (2 thermocouples, one on each side) was measured on two sheep and satisfactory implanted ruminal thermocouple data were available for only two sheep. Heart rate was measured at 10 min intervals using stainless steel pins in the axilla of both forelegs and on the back above the shoulder and was recorded on an ECG (Hewlett Packard, Electrocardiograph Model 1500A). Urine volume was recorded at 10 min intervals.

Mean temperatures and rate of oxygen consumption over 10 min periods were calculated and averaged over 1 h periods for statistical analyses.

The analysis of variance included sheep(3), cooling method (2), cooling level (3) and FED versus NOT-FED (2) as the main fixed sources of variance. These terms were tested against the summation of the variance accounted for by interactions of the main effects with sheep and all three way interactions giving a total of 24 degrees of freedom (df) for error. Time periods (I to IV) during an individual trial were treated as a split-plot within the main treatments and tested against period interactions with sheep plus all three and four way interactions with main effects, giving a total of 93 df for error and a total of 144 observations in each analysis. An example of the analysis

is included in Appendix Ib.

4.1.2 Results and Discussion

4.1.2.1 Method of Rumen Cooling

Records of the flow rate through the coil and temperature differential across the coil showed that the actual rumen cooling achieved by the COIL method was 219 ± 9 kJ and 408 ± 12 kJ for the designed 210 and 400 cooling levels. These values were 4% above and 0.4% below respectively that achieved with INFUSION cooling. The only statistically significant effects of method of rumen cooling were on urine output, rumen temperature and leg skin temperature (Table 4.1).

Urine output was increased approximately tenfold in Period III and IV by the INFUSION cooling treatment. By the end of the 2 h recovery period, 0.63 litres or 25% of the volume of infusate had been recovered over and above the output of urine with the COIL treatment. The energy expenditure of the kidneys is thought to account for only 8% of total M (Baldwin and Smith, 1971). Therefore any increase in energy expenditure of the kidneys due to increased renal filtration was probably small and not detectable with the methods used.

The significant treatment effect on rumen temperature was mainly due to a 2.7°C greater drop during the rumen cooling period with the COIL method. The intra-ruminal thermocouples may have been partially measuring the

Table 4.1 Method of rumen cooling by period interaction means for urine output, leg skin and rumen temperature (Experiment I)

Cooling method	Period ¹				Treatment mean
	I	II	III	IV	
Urine output (ml.min ⁻¹)					
INFUSION	0.4	1.4	5.5	5.5	3.2 ^e
COIL	0.6	0.7	0.7	0.5	0.6 ^f
Rumen core temperature (°C)					
INFUSION	39.1 ^{ae}	36.9 ^{be}	38.1 ^{be}	38.8 ^{ae}	38.2 ^e
COIL	39.0 ^{ae}	34.2 ^{cf}	37.9 ^{be}	38.9 ^{ae}	37.5 ^f
Leg skin temperature (°C)					
INFUSION	27.5	24.5	21.5	21.2	23.7 ^e
COIL	23.0	20.2	17.6	18.6	19.9 ^f

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

¹ Period I = pre-treatment hour, Period II = treatment hour and Periods III and IV = recovery 2x1 hour

temperature of the coil *per se*, rather than the true temperature of the rumen contents, however a lower rumen temperature did persist after the removal of the coil.

Although leg skin temperature (T_{leg}) was 4°C lower with COIL cooling than with the INFUSION cooling method, rumen cooling method did not have a differential effect on the change in T_{leg} . A difference of 4.4°C in T_{leg} between

cooling methods existed in the pre-treatment period for unexplained reasons.

4.1.2.2 Level of Rumen Cooling

Level of rumen cooling had statistically significant effects on all parameters measured with the exception of urine output and trunk skin temperature.

Body and Rumen Temperatures

Three examples of significant ($p < 0.05$) rumen cooling level by period interactions are shown in Table 4.2. The time course change for rectal, leg skin and rumen temperature for the NIL and HIGH cooling levels are shown in Figure 4.1.

During the 4 h trial, body and rumen temperatures of sheep receiving the NIL level of rumen cooling remained constant or showed a slight rise. LOW and HIGH rumen cooling levels induced a decline in body and rumen temperatures, with the decline due to the HIGH level of cooling being approximately twice that induced by the LOW rumen cooling level. Rectal temperature fell 0.7 and 1.5 °C with LOW and HIGH cooling levels respectively and reached these levels *before* extremity skin temperatures had declined to their minimum levels. It is probable that the T_{ear} and T_{leg} recorded for the HIGH cooling level in Period IV reflected minimum extremity skin temperature in a T_a of 10°C (Blaxter et al., 1958b). Any linear decline in body temperatures with increasing cooling level will ultimately

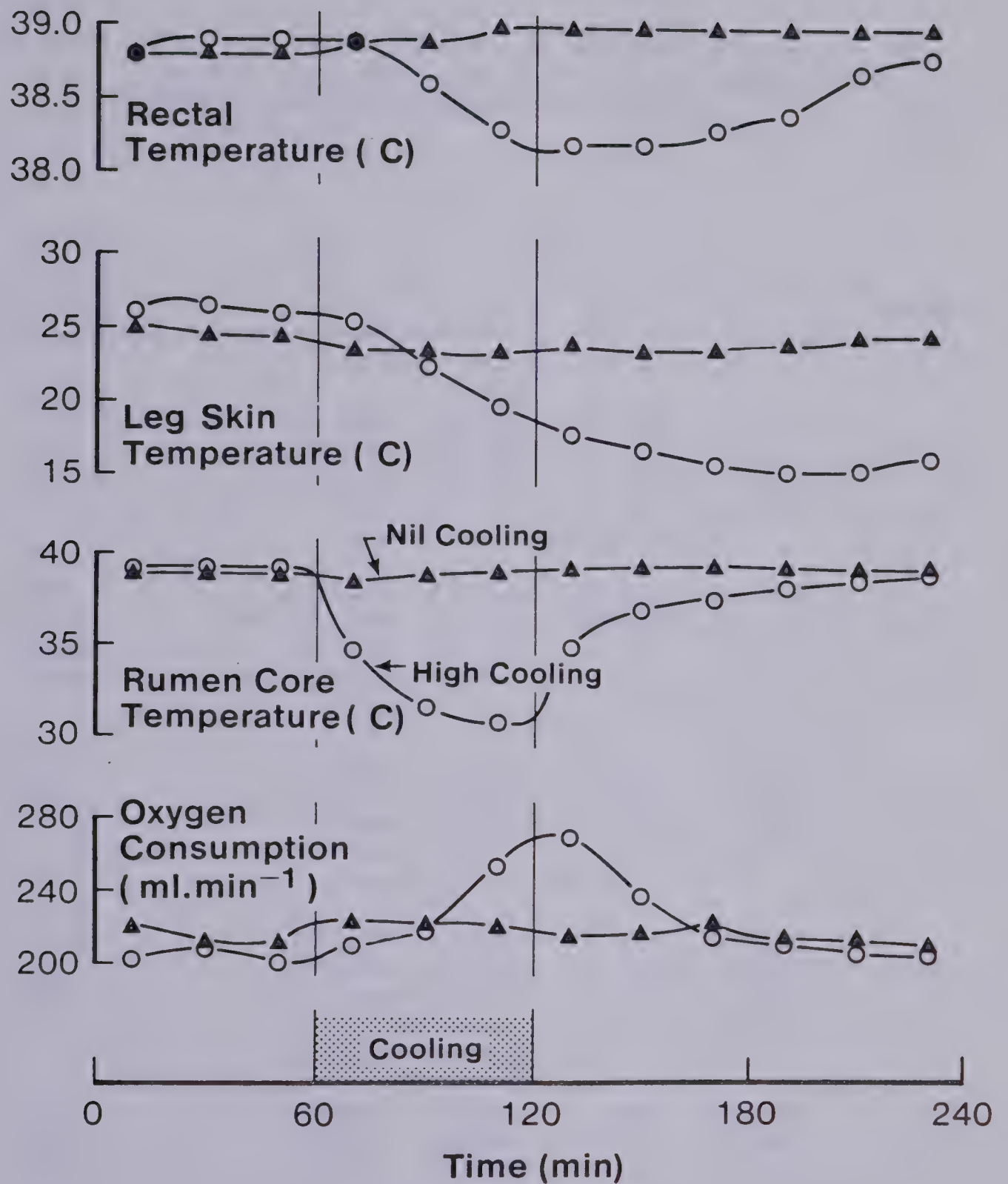


Figure 4.1 Time course change in rectal, leg skin and rumen temperature and oxygen consumption of sheep receiving NIL (solid symbols) or HIGH (open symbols) levels of rumen cooling (Experiment I)

Table 4.2 Cooling level by period interaction means for rectal, leg skin and rumen core temperature, heart rate and oxygen consumption (Experiment I)

Level of cooling	Period				±SEM
	I	II	III	IV	
Rectal temperature (°C)					
NIL	38.8 ^{ae}	38.9 ^{ae}	39.0 ^{ae}	39.0 ^{ae}	0.04
LOW	38.8 ^{ae}	38.6 ^{abf}	38.5 ^{bf}	38.8 ^{ae}	
HIGH	38.9 ^{ae}	38.5 ^{bcf}	38.3 ^{bcf}	38.7 ^{abf}	
Leg skin temperature (°C)					
NIL	24.4 ^{ae}	23.4 ^{ae}	23.4 ^{ae}	24.5 ^{ae}	0.84
LOW	24.9 ^{ae}	21.7 ^{abe}	18.8 ^{abf}	20.1 ^{abf}	
HIGH	26.4 ^{ae}	21.9 ^{be}	16.5 ^{cf}	15.7 ^{cg}	
Rumen core temperature (°C)					
NIL	39.0 ^{ae}	38.8 ^{ae}	39.3 ^{ae}	39.3 ^{ae}	0.33
LOW	38.9 ^{ae}	35.6 ^{bfe}	37.8 ^{af}	38.9 ^{af}	
HIGH	39.2 ^{ae}	32.1 ^{cg}	36.9 ^{bg}	38.6 ^{af}	
Heart rate (beats.min ⁻¹)					
NIL	78.5 ^{ae}	88.0 ^{be}	78.9 ^{ae}	75.8 ^{ae}	1.42
LOW	76.4 ^{ae}	90.1 ^{be}	84.7 ^{abe}	76.6 ^{ace}	
HIGH	76.1 ^{ae}	92.2 ^{be}	97.8 ^{bf}	80.9 ^{ae}	
Oxygen consumption (ml.min ⁻¹)					
NIL	217 ^{ae}	223 ^{ae}	219 ^{ae}	206 ^{ae}	4.0
LOW	208 ^{ae}	225 ^{ae}	235 ^{bef}	213 ^{ae}	
HIGH	204 ^{ae}	221 ^{ae}	245 ^{bf}	206 ^{ae}	

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

be limited by this minimum temperature.

Although T_r had recovered considerably by Period IV, the computed T_b of 36.6, 36.1 and 35.7°C for the NIL, LOW and HIGH cooling levels respectively were all significantly ($p < 0.05$) different in Period IV. and T_b with the LOW and HIGH levels of rumen cooling was still significantly below the pre-cooling (Period I) level. Thus two hours after rumen cooling stopped the sheep were considerably rumen cooler than before the cooling took place.

Site of Rumen Temperature Measurement

Temperatures recorded over Period II at five ruminal sites are shown in Table 4.3. With the NIL cooling level the steady state between intra- and extra-ruminal (on the abdominal surface of the rumen) temperatures was not disrupted. With the LOW and HIGH levels considerable temperature gradients of 1.8 and 2.7°C were established and were indicative of heat flow into the rumen from the body. Extra-ruminal temperatures were 1.7 to 2.0°C below rectal temperature.

Gradients of up to 6.0°C were established between the rumen core and deep body temperature and approximately 50% of this gradient occurred across the rumen wall.

Heart Rate and Oxygen Consumption

Heart rate increased in Period II due to eating (see next section) but was further increased in Periods II and III with the LOW and HIGH levels of rumen cooling (Table

Table 4.3 Rumen temperature recorded at five sites as influenced by level of rumen cooling in Period II (Experiment I)

Rumen temperature (°C)	Cooling level			±SEM
	NIL	LOW	HIGH	
Core	38.8a	35.6b	32.1c	0.16
Dorsal sac				
intra ¹	39.0a	34.4b	34.1b	0.19
extra	38.9a	36.7b	36.4b	0.19
Ventral sac				
intra	38.9a	35.7b	33.6c	0.16
extra	38.9a	37.0b	36.7b	0.14

a, b, c, d means in rows followed by the same letter are not significantly different ($p < 0.05$)

¹ intra = thermocouple inserted through the rumen wall into the lumen of the rumen
extra = thermocouple on the abominal surface of the rumen

Differences within columns not statistically analysed.

4.2). Oxygen consumption was significantly elevated due to cooling treatment only in Period III. The LOW and HIGH cooling treatments increased oxygen consumption by 13 and 20% respectively. The cumulative increase in oxygen consumption during Period II to IV above the NIL cooling level totalled 58 and 75 kJ for the LOW and HIGH cooling levels; equivalent to 18 and 28% of the rumen cooling respectively.

Overt shivering was only observed with the HIGH cooling level and a marked increase in \dot{M} did not occur until the final 30 min of the rumen cooling period, but continued for 10 to 15 min after cooling stopped. Shivering therefore occurred before minimum skin temperatures had been achieved.

Urine Output

There was no consistent effect of cooling level on urine output, the overall mean being $1.9 \text{ ml} \cdot \text{min}^{-1}$. Body fluid shifts, likely to induce an increase in urine volume, have been shown to occur over a period of days in sheep exposed to low ambient temperatures (Degen and Young, 1979). The collection period in this experiment was probably of insufficient length to measure any change in urine output due to changes in body fluid compartmentation in response to rumen cooling.

4.1.2.3 FED versus NOT-FED Treatment

Feeding treatment significantly affected all temperatures recorded except leg skin, trunk skin and rectal temperatures. In general, body and rumen temperatures declined less when rumen cooling was accompanied by eating but metabolic rate increased with feeding (Figure 4.2). Changes in temperature with and without associated feeding are shown in Table 4.4. The smaller change in body temperature when cooling was accompanied by eating was reflected in a significant ($p < 0.05$) interaction between feeding treatment and period (Table 4.5). The decline in

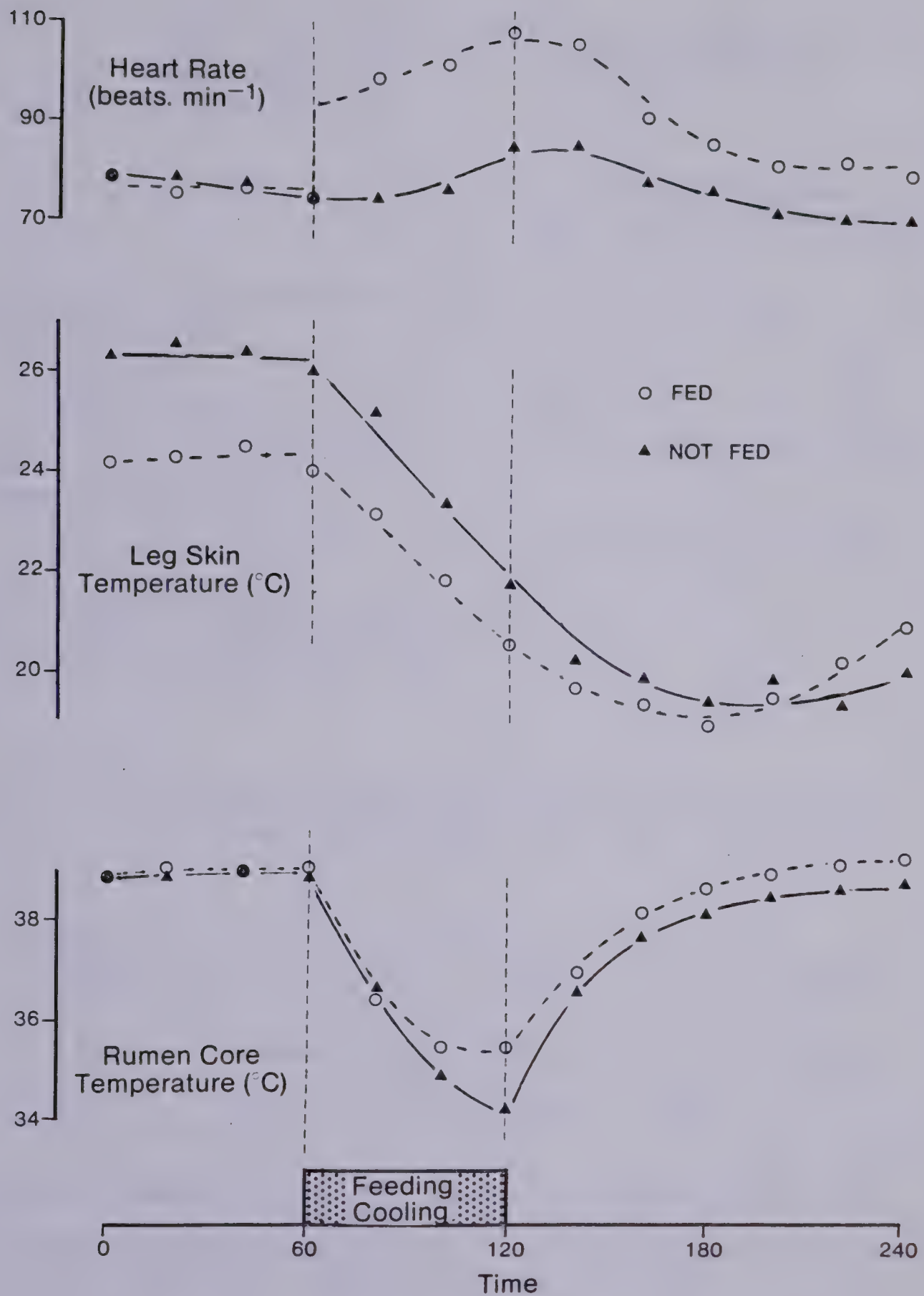


Figure 4.2 Time course change in heart rate, leg skin and rumen core temperature of FED (broken line) and NOT FED (solid line) rumen cooled sheep (Experiment I)

Table 4.4 Effect of feeding treatment on change in ear skin, leg skin and rumen core temperature, heart rate and oxygen consumption (Experiment I)

	Feeding Treatment	
	FED	NOT FED
Temperature ($^{\circ}\text{C}$)		
ear skin ¹	+1.6	-11.8
leg skin ¹	-3.8	-6.4
rumen core ²	-4.5	-5.8
Heart rate (beats.min ⁻¹) ³	+0.7	+25.5
Oxygen consumption ³ (ml.min ⁻¹)	+4	+22

¹ change Period I through IV

² maximum change Period I to II

³ mean change Period I to II

Table 4.5 Feeding treatment by period interaction means for mean body temperature ($^{\circ}\text{C}$) (Experiment I)

Feeding treatment	Period				$\pm\text{SEM}$
	I	II	III	IV	
FED	36.4 ae	36.3 ae	36.1 ae	36.3 ae	0.07
NOT-FED	36.6 ae	36.4 ae	35.8 bf	36.0 bf	

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

mean body temperature in the FED treatment was about 50% of that recorded in the NOT-FED treatment.

Urine Output

Urine output was significantly ($p < 0.05$) reduced by 24% during Periods II, III and IV in the FED treatment. A decline in urine production with feeding has been observed (Blair-West and Brook, 1969) and is associated with the reduction in plasma volume which has been shown to coincide with feeding a dry ration (Christopherson and Webster, 1972). There was no interaction between method of cooling and feeding, so the reduction in urine output was consistent over both the INFUSION and COIL cooling methods.

Although the water infused into the rumen could not have substituted for saliva flow into the rumen, it might have been expected to substitute for any net flow of water across the rumen wall into the rumen (Ternouth, 1968) in response to increased rumen osmolarity with feeding (Warner and Stacey, 1965). Considering the volume of water (1.25 litres on average) which was infused into the rumen it is somewhat surprising that urine volume was reduced with feeding.

Heart Rate and Oxygen Consumption

During the feeding period the increases in heart rate and oxygen consumption were 30 and 9% respectively over the NOT-FED values. The increase in heart rate was similar to that recorded during feeding by Christopherson and Webster (1972) but the increase in oxygen consumption is much lower

than that normally associated with the feeding response of 30 to 50% (Young, 1966; Christopherson and Webster, 1972; Osuji et al., 1975). Heart rate in this experiment was recorded at the beginning of each 10 min period immediately after the sheep were fed. The sheep consumed the 42 g feed offered at 10 min intervals in 1 to 2 min, or one fifth of the time. The smaller increase in oxygen consumption with eating probably reflected this sporadic feeding pattern.

4.1.3 General Discussion Experiment I

4.1.3.1 Mass plus heat versus heat

For an effective cooling of the rumen by 210 kJ, the INFUSION cooling method added 2.5 kg of mass as water and 198 kJ of heat, whereas COIL cooling removed 219 kJ directly from the rumen. The calculated theoretical drop in rumen temperature for each cooling rate as a result of these heat and mass exchanges if no heat was transferred from the body have been calculated for a range of rumen mass (Table 4.6).

The observed difference between the two cooling methods at the end of the cooling period was 2.7 and 5.4°C. Rumen volumes of 5.8 and 5.4 litres would be predicted from the difference between the cooling methods for the 210 and 400 cooling treatments respectively. Differential rates of movement of rumen contents from the rumen with the two treatments during cooling should not influence such a

Table 4.6 Theoretical rumen temperature ($^{\circ}\text{C}$) at the end of rumen cooling by the two experimental methods (Experiment I)

Rumen volume (litres)	Cooling Method ¹		Difference
	INFUSION	COIL	INFUSION-COIL
LOW cooling treatment			
4	31.3	26.5	4.8
5	32.3	29.0	3.3
6	33.1	30.6	2.5
7	33.7	31.8	1.9
HIGH cooling treatment			
4	24.4	15.2	9.2
5	26.3	20.0	6.3
6	27.8	23.2	4.6
7	29.0	25.4	3.6

Assumptions Specific gravity of rumen fluid = 1.0
 Specific heat of rumen fluid = 1.0
 Pre-cooling rumen temperature = 39.0°C

¹ INFUSION cooling method = rumen infusion
 of 2.5 litres water over 1 hour at 19°C
 (LOW) or at 2°C (HIGH)

COIL cooling method = 210 kJ (LOW) or 400 kJ
 (HIGH) heat removed from the rumen
 over 1 h with a cooling coil

calculation of rumen volume if the mass leaving was at the mean rumen temperature.

A difference of $>5^{\circ}\text{C}$ in rumen temperature between the methods of cooling would not be expected unless the increase in rumen volume due to the infusion of water was $>40\%$ and the temperature differential between the added cold mass and the rumen was $>38^{\circ}\text{C}$. Within these limits either cooling

method could be used in experiments studying HW without fear of undue bias due to the cooling method used.

4.1.3.2 Heat gained by the rumen

The total heat gained by the rumen from the body over the cooling period was estimated from the difference between the theoretical (Table 4.6) and the actual temperature of the rumen at the end of the cooling period. A pre-cooling rumen volume of 5.4 and 5.8 litres for the HIGH and LOW cooling levels was used. The result of this calculation is shown in Table 4.7.

Table 4.7 Calculated heat gain (kJ) by the rumen in response to rumen cooling over 1 hour (Experiment I)

Cooling treatment	Method of Cooling			
	INFUSION		COIL	
	kJ	%	kJ	% ¹
LOW ²	134	63.8	92	43.8
HIGH	255	63.8	159	39.8

¹ Heat gained by rumen as % rumen cooling

² LOW 210 kJ rumen cooling over 1 h
 HIGH 400 kJ rumen cooling over 1 h

Estimation of heat gained by the rumen using COIL data tended to under-estimate the actual heat gain since no allowance was made for an increase in rumen volume over the cooling period due to saliva and feed. Conversely, the estimate from the INFUSION cooling method may over-estimate

the heat flow into the rumen since it does not account for a decrease in volume due to a potential efflux of the infusate across the rumen wall. If COIL post-cooling rumen volume was increased by 0.3 to 0.4 litres and INFUSION rumen volume decreased by a similar volume, both methods would estimate that approximately 50% of the cooling was recovered by the rumen over the one hour cooling period.

4.1.3.3 Association of feeding with rumen cooling

The impact of feeding on the response to ruminal cooling is summarised in Figure 4.3 which shows the change in T_b and M from Period I, relative to the changes in the NOT-FED, NIL cooling treatment. The following points may be noted.

1. Feeding in the absence of rumen cooling increased T_b and Tru in Periods III and IV.
2. Rumen cooling completely negated this increase and body and rumen temperatures declined.
3. In Period III and IV there appears to have been substitution of the body temperature rise due to feeding for the fall in temperature with rumen cooling. The substitution ranged from 38 to 138% with a mean of 81%. A similar substitution of the rise in rumen temperature with feeding for the decline in rumen temperature with rumen cooling was evident, but the substitution was not as large (40%).
4. In contrast to body and rumen temperatures, the

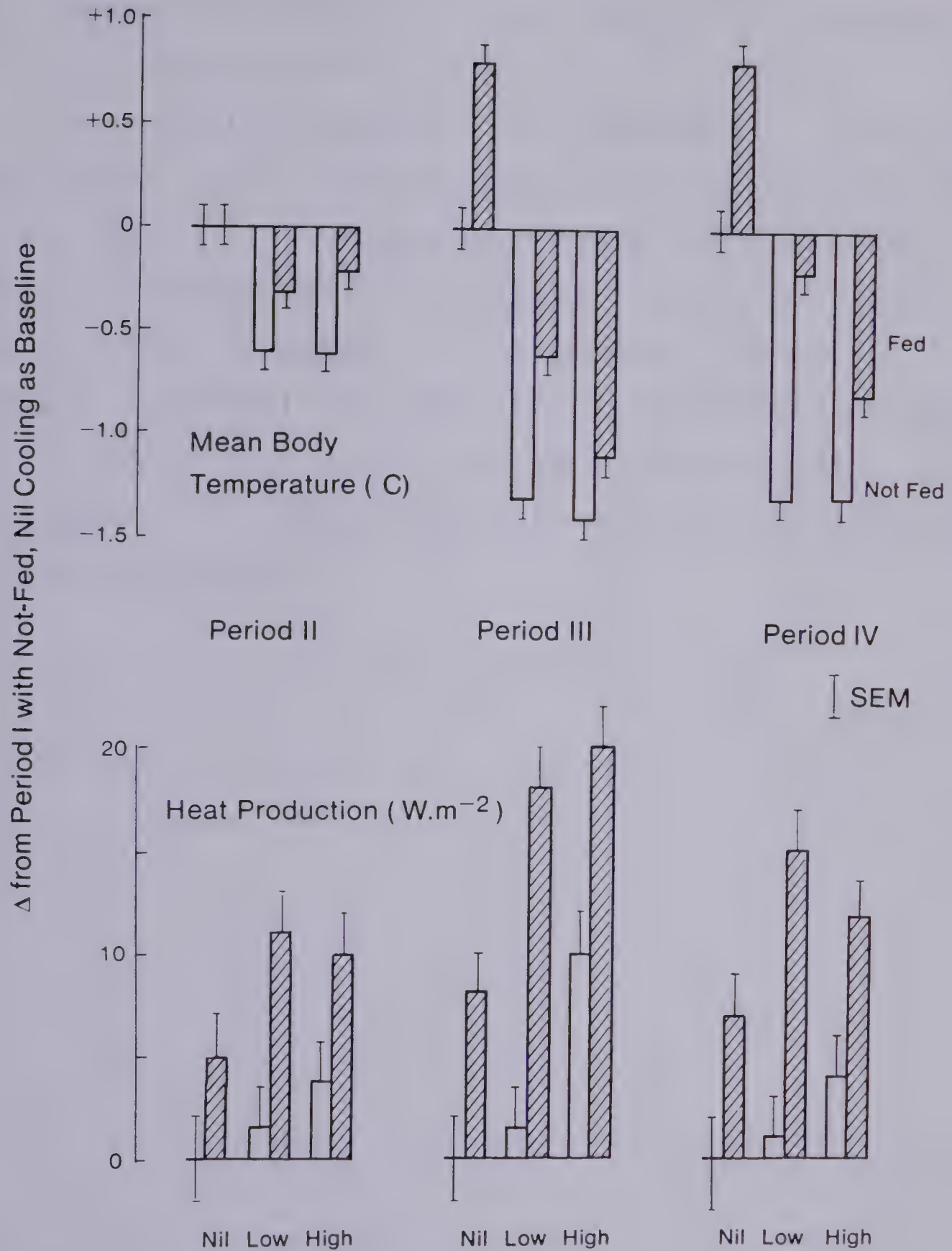


Figure 4.3 Relative change in mean body temperature and heat production between FED and NOT FED sheep from Period II through Period IV (NOT FED, NIL cooling used as baseline (Experiment I) (FED treatment hatched area)

increase in heat production with feeding did not appear to substitute for the rise in heat production in response to cooling.

The cumulative increase in M in Periods II, III and IV, over Period I in the NOT-FED treatment was equivalent to 20% of the cooling. The cumulative increase in M with rumen cooling, over and above that caused by feeding was a similar 26% in the FED treatment. If the increase in M due to feeding is included, the cumulative increase in M in Periods II, III and IV could account for 45% of HW in the FED treatment. This lack of substitution may be a reflection of the sporadic eating.

4.2 Experiment II Rate and timing of rumen cooling

Rumen cooling treatments in Experiment I were a combination of a variable total quantity (HW) and variable rate (G) of cooling. The effect of rumen cooling on body temperature was reduced when the cooling was accompanied by feeding but the increase in body temperatures due to feeding occurred *after* cooling. In Experiment II one level of rumen cooling was imposed at three rates to determine the effect of rate of cooling per se and rumen cooling during feeding was compared with cooling after feeding.

4.2.1 Experimental Treatments and Measurements

The following treatments were incorporated in a 3x3x2 randomised block design using three sheep, three rates of rumen cooling and rumen cooling at two times relative to feeding.

4.2.1.1 Rate of Rumen Cooling Treatment

Three rates of rumen cooling were compared.

1. FAST

116 W of rumen cooling for the first 30 min of Period II.

2. MEDIUM (MED)

58 W of rumen cooling for 60 min (Period II)

3. SLOW

29 W of rumen cooling for 120 min (Periods II and III)

All three rate of cooling treatments were equivalent to a total cooling of 210 kJ.

4.2.1.2 Time of Rumen Cooling Treatment

Rumen cooling was applied at two times relative to feeding.

1. DURING FEEDING

Cooling imposed during feeding as described in Experiment I.

2. POST-FEEDING

Cooling imposed 30 min after the conclusion of feeding.

Rumen cooling was by the intra-ruminal cooling coil method described in Experiment I. Oxygen consumption, rectal temperature, ear, leg and trunk skin (2) temperatures and rumen core temperature were recorded continuously over each four hour trial.

For evaluating the effects of the rate of cooling treatment on body and rumen temperatures the following data were used

1. Pre-cooling - Mean of the two 10 min periods immediately prior to rumen cooling.
2. End of cooling - The mean of the final 10 min of

the cooling period.

3. 1 h post-cooling - Values 1 h after those recorded in (2).
4. 3 h after the start of cooling - Values for the 10 min period equivalent to 150, 120 and 60 min after cooling stopped.

For the time of cooling treatment, the means of Periods I to IV were compared as in Experiment I.

The recovery in rumen temperature with time after the end of cooling was approximated by an exponential curve (Figures 4.1 and 4.2). The natural logarithm of the difference between rumen temperature before cooling and at 10 min intervals post-cooling was fitted by regression analysis against time.

4.2.2 Results and Discussion

4.2.2.1 Rate of Cooling

Rate of rumen cooling significantly affected rectal, leg skin and rumen temperature and oxygen consumption.

Body Temperatures

Faster rates of cooling induced greater declines in body temperature, but showed greater recovery within the time frame of the experiment (Table 4.8). Figure 4.4 shows graphically the changes in T_b . The rate of decline in mean body temperature was dependent on the rate of rumen cooling. Mean body temperature declined 13, 10 and $4 \times 10^{-3} \text{ } ^\circ\text{C}.\text{min}^{-1}$

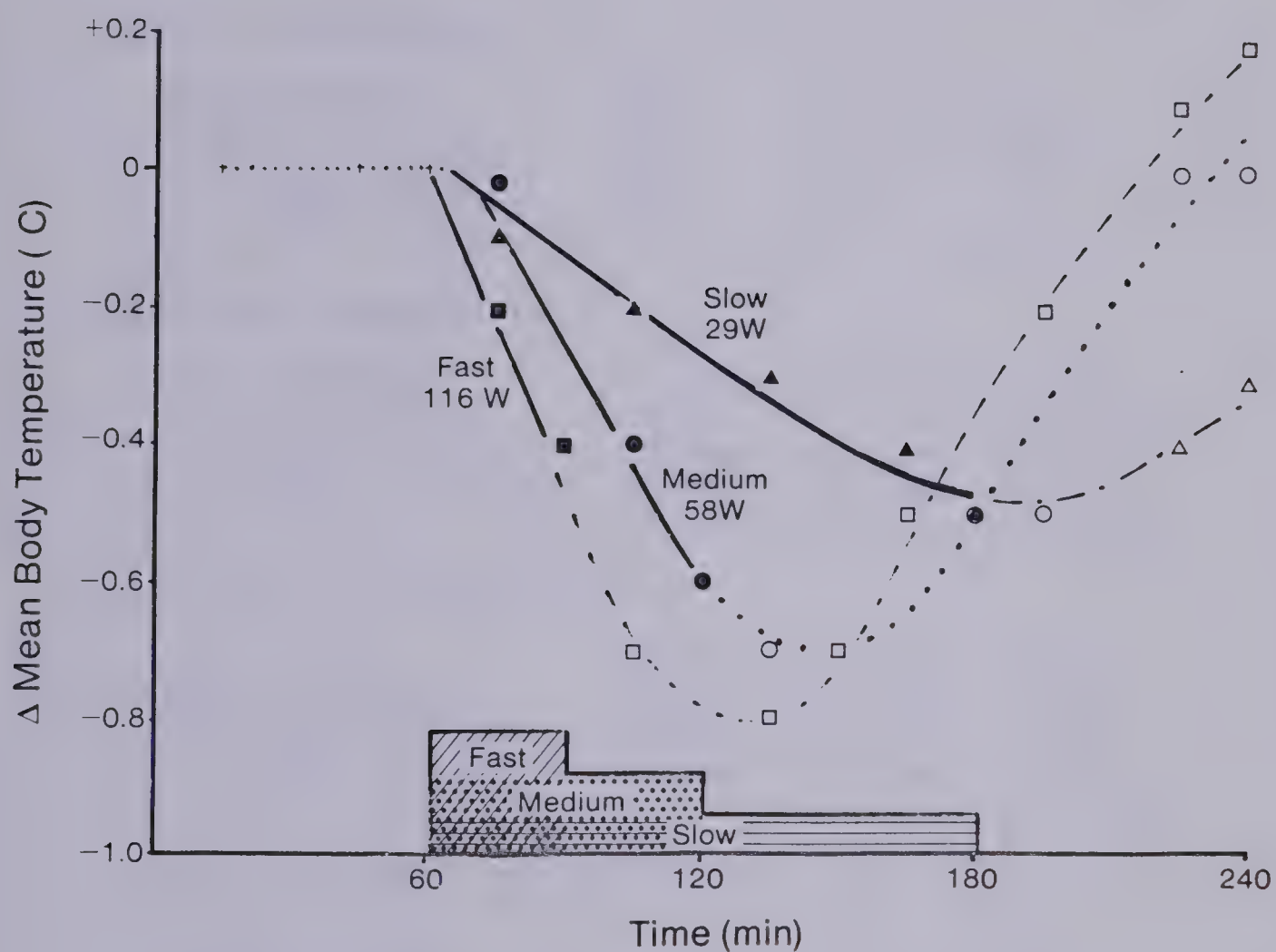


Figure 4.4 Effect of rate of rumen cooling on change in mean body temperature of sheep (Experiment II) (solid lines, cooling phase; broken line, recovery phase)

Table 4.8 Effect of rate of rumen cooling on rectal, mean body and rumen temperatures and rumen temperature kinetics (Experiment II)

	Rate of cooling		
	SLOW	MEDIUM	FAST
Rectal temperature (°C)			
Pre-cooling	39.0	39.0	39.0
End of cooling	38.9	38.7	38.9
1 h post-cooling	39.0	38.8	39.0
3 h after cooling	39.0	39.1	39.1
Mean body temperature (°C)			
Pre-cooling	37.2 _{ae}	36.9 _{ae}	37.0 _{ae}
End of cooling	36.7 _{ae}	36.3 _{ae}	36.9 _{ae} _f
1 h post-cooling	36.9 _{ae}	36.4 _{ae}	36.3 _{ae} _f
3 h after cooling	36.9 _{ae}	36.9 _{ae}	37.2 _{ae}
Rumen core temperature (°C)			
Pre-cooling	39.7 _{ae}	39.5 _{ae}	39.7 _{ae}
End of cooling	36.9 _{af}	35.2 _{bf}	33.4 _{cf}
1 h post-cooling	39.3 _{ae}	39.1 _{ae}	39.1 _{ae}
3 h after cooling	39.3 _{ae}	39.6 _{ae}	39.6 _{ae}
Kinetics of rumen temperature recovery			
Time constant (10 ⁻³ .min ⁻¹)	33.6	41.1	41.7
T 1/2 (min)	21	17	17
Predicted max. temp. drop (°C)	2.6	4.4	5.9

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

which was equivalent to a rate of loss of body heat content (\dot{S}) of 36, 21 and 11 W for the FAST, MED and SLOW rates of cooling respectively. Mean body temperature continued to fall for 10 to 30 min after cooling ceased. At minimum T_b the total loss in body heat content (HC) was 130, 114 and 81 kJ for the FAST, MED and SLOW treatments respectively and was equivalent to 62, 54, and 38% of the rumen cooling.

By 1 h post-cooling, some recovery in T_b had taken place. Due mainly to the variable length of time for recovery before the end of the trial, the residual effects of the SLOW rate of cooling were greater.

Rumen Temperature Recovery

Although the fall in rumen temperature during cooling was significantly ($p < 0.05$) affected by rate of rumen cooling, the time constants for the recovery of T_{ru} were very similar. Half of the decrease in T_{ru} was recovered in 17 to 21 min (Table 4.8). Diffusion of heat into the rumen would appear to be mainly a function of the temperature gradient between the rumen and the body core.

Oxygen Consumption

Differences in oxygen consumption due to rate of cooling were confounded by cooling ending at a different time after feeding with each rate of cooling and by the inexplicably high pre-cooling rate of oxygen consumption in sheep subsequently receiving the FAST cooling rate (Table 4.9).

Table 4.9 Rate of rumen cooling by time period interaction on oxygen consumption ($\text{ml} \cdot \text{min}^{-1}$)

Rate of cooling	Period			
	I	II	III	IV
SLOW	211 ae	223 ae	229 ae	221 ae
MEDIUM	204 ae	229 be	223 abe	215 abe
FAST	245 af	252 af	235 ae	231 ace

a, b, c, d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e, f, g, h means in columns followed by the same letter are not significantly different ($p < 0.05$).

Oxygen consumption during Periods II and III, above the mean of Periods I and IV showed a total increase equivalent to 13, 40 and 24 kJ for the FAST, MED and SLOW rates respectively, suggesting that the MED cooling may have been more effective in stimulating metabolic rate.

4.2.2.2 Time of cooling

Body Temperatures

Feeding established higher body temperatures before cooling (Table 4.10). The decline in body temperatures with cooling was greater when the sheep were fed before cooling but the recovery of body temperatures after cooling was less when the sheep were fed before rumen cooling.

Although the drop in body temperatures was greater with the POST feeding treatment and the recovery in body temperatures after cooling was less, all final body

Table 4.10 Time of feeding treatment by period interaction means for rectal, ear skin, mean body and rumen core temperature (Experiment II)

	Period			
	I	II	III	IV
Rectal temperature (°C)				
DURING ¹	38.9 ae	38.9 ae	38.9 ae	39.1 bf
AFTER	39.1 ae	39.0 abe	38.9 be	38.9 be
Ear skin temperature (°C)				
DURING	26.1	24.4	20.3	22.5
AFTER	32.2	29.7	23.1	24.2
Mean body temperature (°C)				
DURING	36.6 ae	36.5 ae	36.4 ae	36.7 ae
AFTER	37.3 af	37.1 abf	36.7 ce	36.8 bce
Rumen core temperature (°C)				
DURING	39.2 ae	36.5 ce	38.2 be	39.4 ae
AFTER	39.8 af	36.9 ce	37.8 be	39.1 ae

¹ DURING = Rumen cooling during eating
 AFTER = Rumen cooling 30 min after eating

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)
 e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

temperatures were slightly greater at the end of the trial for the sheep cooled during feeding.

Mean body temperature, representing the net effect of changes in body temperatures was compared between Experiments I and II (Table 4.11).

Table 4.11 Mean body temperature ($^{\circ}\text{C}$) pre- and post-rumen cooling as influenced by the time of cooling in relation to feeding (Experiments I and II)

Time	Experiment I		Experiment II	
	NOT-FED	FED	DURING	POST
Pre-Cooling	36.6	36.4	36.6	37.3
Post-cooling	35.8	36.1	36.4	36.7
Pre minus Post	-0.8	-0.3	-0.2	-0.6

Cooling without feeding (NOT-FED, Experiment I) or cooling after feeding (POST, Experiment II) caused a similar decline in T_b which was more than twice that when cooling accompanied feeding (FED, Experiment I and DURING, Experiment II). This change in T_b represents a mean change in HC of 41 kJ when feeding accompanied cooling and 114 kJ when the cooling was not associated with eating. With rumen cooling post-feeding, T_b declined from an initially *high* level to a value similar to that achieved with cooling during feeding. On the other hand, the decline in T_b when cooling was not accompanied by feeding at any stage was to a level well *below* the other treatments.

Oxygen Consumption

The confounding of time of cooling with time of feeding in this experiment makes a direct interpretation of the oxygen consumption data difficult. However a comparison of the oxygen consumption from similar cooling treatments in Experiments I and II has been made (Table 4.12). The increase in oxygen consumption with 210 kJ of rumen cooling was similar in both experiments where cooling was synchronous with feeding. The pattern of oxygen consumption of the POST treatment is similar to the NIL cooling treatment in Experiment I. No appreciable increase in oxygen consumption was observed during cooling when cooling occurred after feeding. A very similar pattern in heart rate between the above treatments can also be shown (see Appendix II).

Table 4.12 Oxygen consumption (ml.min⁻¹) over 30 min sub-periods with cooling treatments (Experiments I and II)

Experiment	Treatment		1	2	3	4	Sub-period				9	10
	Cooling	feeding					5	6	7	8		
(1) I	LOW	FED	198	206	221	246	260	243	225	229	---	---
(2) II	LOW	DURING	215	207	215 cooling and feeding	248	252	237	233	230	---	---
(3) II	LOW	POST	---	---	---	226	230	230 cooling	230	222	222	226
(4) I	NIL	FED	218	214	227 feeding	230	235	233	228	209	---	---

Note:- Feeding occurred in all experimental treatments during sub-periods 3 and 4
Rumen cooling (210 kJ) occurred during sub-periods 3 and 4 in cases (1) and (2)
Rumen cooling (210 kJ) occurred during sub-periods 6 and 7 in case (3)
There was no rumen cooling in (4)

4.3 Experiment III Feed intake and insulation effects on the heat of warming

Higher feed intakes elevate body temperatures (Blaxter et al., 1958b) and shearing reduces mean body temperatures, at least for a few days after shearing (Webster, 1966; Webster and Johnson, 1968). Shearing may be a practical situation where any deleterious effects of HW are exacerbated. The effects of rumen cooling were reduced by an elevation in body temperatures due to feeding (Experiments I and II) but the rise in body temperatures with feeding only existed for one to two hours. If longer-term higher body temperatures could be established, the impact of the heat of warming might be further reduced.

Experiment III compared two levels of rumen cooling imposed on woolly and shorn sheep at low and high feed intakes.

4.3.1 Experimental Treatments and Measurements

The experimental treatments were:-

4.3.1.1 External Insulation - Feed Intake Treatments

Three external insulation (fleece length)-feed intake combinations were compared.

1. Woolly sheep at low feed intake (WOOLLY-LOW)

Woolly sheep (10 to 12 cm fleece length) were established on a feed intake of 500 g Ration A daily

for 8 days before the rumen cooling trials

2. Woolly sheep at high feed intake (WOOLLY-HIGH)

Woolly sheep were established on a feed intake of 1250 g Ration A per head per day for 8 days before rumen cooling trials were conducted.

3. Shorn sheep at high feed intake (SHORN-HIGH)

Woolly sheep at the high feed intake were shorn (0.5 cm fleece depth) and exposed to rumen cooling trials on two consecutive days after shearing.

Each sheep moved sequentially through the Feed Intake - Insulation treatments in the above order.

4.3.1.2 Level of Cooling

Two levels of cooling, the LOW and HIGH treatments as described in Experiment I, were used. The cooling method was by intra-ruminal water infusion. The cooling levels were allocated at random.

Two sheep were used in the 2x3x2 partially randomised block design. Each trial consisted of the same four 1 h periods as described for Experiment I with feeding (250 g Ration A) and cooling during the second hour (Period II) of each trial. The same measurements were made as for Experiment II and the data were statistically analysed as for Experiment I.

4.3.2 Results and Discussion

4.3.2.1 Feed Intake and Insulation

Major differences in body temperatures, heart rate and \dot{M} existed between the main treatments prior to cooling (Table 4.13). Woolly sheep on the high feed intake had higher initial body temperatures and heat production than woolly sheep at the low feed intake. Shorn sheep had lower initial body temperatures than the woolly sheep and a higher rate of heat production than the woolly-high intake treatment.

In common with the results from Experiments I and II, all body temperatures declined in response to ruminal cooling with lowest body temperatures being reached in Period III and some recovery being shown by Period IV. The trend was for the maximum decline in extremity skin temperature to be greatest for the woolly well-fed sheep and least for the shorn well-fed sheep.

Since the oxygen consumption of the shorn sheep was 30% higher than the woolly sheep at the same feed intake, the shorn sheep were considered to be out of thermoneutrality. Peripheral vaso-constriction is normally considered to be at a maximum below the critical temperature of an animal. However rumen cooling of the shorn sheep did induce a decline in extremity skin temperature. This observation suggests that the stimulation of rumen and deep body thermo-receptors induced further vaso-constriction which might have been expected to already be at a maximum.

Table 4.13 Pre-cooling and maximal change in ear, leg, and mean body temperatures, heart rate oxygen consumption (Experiment III)

	Insulation treatment-feed intake ¹		
	WOOLLY-HIGH	WOOLLY-LOW	SHORN-HIGH
Ear skin temperature (°C)			
Pre-cooling	34.0a	19.8b	20.7a
Max. change	-13.9	-7.2	-5.9
Leg skin temperature (°C)			
Pre-cooling	26.8a	16.9b	17.4a
Max. change	-9.6	-5.1	-4.8
Mean skin temperature (°C)			
Pre-cooling	31.0	30.7	25.7
Max. change	-2.1	-0.4	-1.0
Heart rate (beats.min ⁻¹)			
Pre-cooling	87a	54b	98c
Max. change	+17	+36	+50
Oxygen consumption (ml.min ⁻¹)			
Pre-cooling	249a	170a	337b
Max. change	+33	+51	+150

a,b,c,d means in rows followed by the same letter are not significantly different (p<0.05)

¹ WOOLLY = fleece depth 10 to 12 cm
SHORN = fleece depth 0.5cm (shorn)

HIGH = 1250 g Ration A daily
LOW = 500 g Ration A daily

Despite the greater drop in body temperature with rumen cooling at the higher feed intake and superior insulation, the post-cooling temperatures were still higher than with the lower feeding level and inferior insulation. The cumulative increase in M during Periods II, III and IV above Period I was equivalent to only 40 kJ with the woolly well-fed sheep compared with 98 and 173 kJ with the woolly sheep at the low feed intake and the shorn sheep respectively. This increase in M was equal to 13, 32 and 57% of the rumen cooling.

4.3.2.2 Cooling Level

Very similar trends in body and rumen temperature changes with cooling level occurred as in Experiment I. In this experiment, T_b fell 0.4°C with the lower level of cooling and 0.7°C with the higher level. The corresponding values from Experiment I were 0.6 and 0.9°C for the LOW and HIGH cooling respectively.

4.4 General Discussion Experiments I, II and III

4.4.1 Change in Body Heat Content

Changes in mean body temperature (T_b) reflect changes in body heat content if body mass and specific heat remain the same and no large internal temperature gradients exist.

In these experiments considerable changes in T_b occurred in response to the various rumen cooling regimes imposed in Experiments I, II and III. The decline in heat content of the animal with ruminal cooling, and its regain after cooling represents a reserve or 'bank' of heat which has potential as a thermal buffer against the impact of internal cooling via the rumen.

To estimate the extent to which the heat content buffer played a part in the overall response to ruminal cooling in these experiments, the net change in HC from Period I through Period IV was calculated for all the main treatment effects. By the end of Period IV, rumen temperature was within 0.5°C of rectal temperature and thus calculation of HC would not be affected by temperature gradients within the body. Fleece-free body weight was used to calculate HC and the specific heat of the body tissues was taken as 0.83 (see Minard, 1970).

The net change in heat content from Period I through Period IV is shown in Figure 4.5 for the main treatment effects. Salient points are:

1. In all cases where rumen cooling occurred, body heat content was lower 2 h post-cooling than before rumen cooling took place. The net reduction in HC of the sheep in response to the 400 kJ rumen cooling was approximately 160 kJ or 40% of the cooling.
2. Feeding activity reduced the body heat debt due to cooling by 65 to 70 kJ.

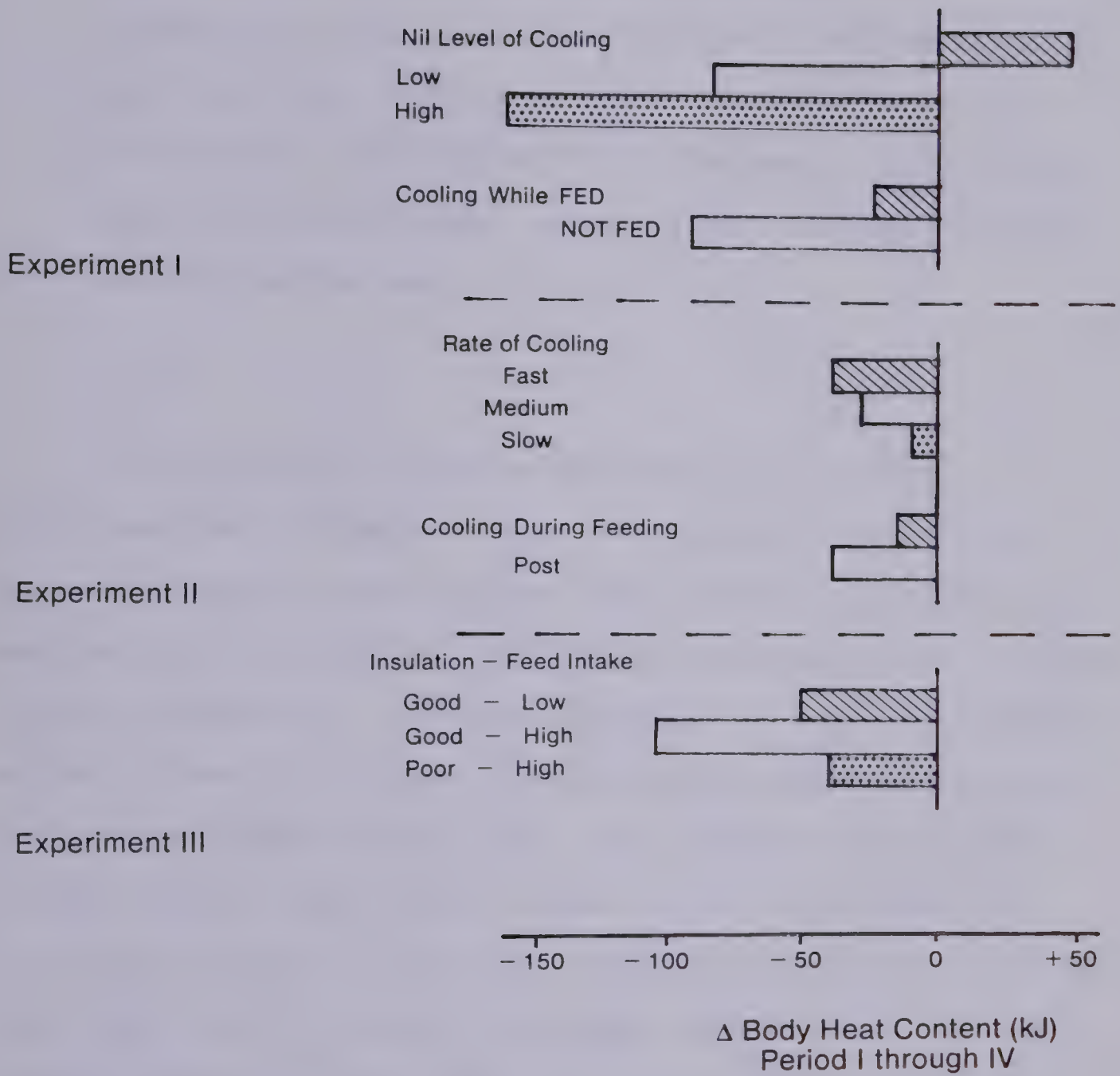


Figure 4.5 Net change in body heat content of sheep from Period I through Period IV (Experiment I-III)

3. Where body temperatures were high before the cooling (eg. in treatments where rumen cooling took place after feeding, Experiment II or where the level of feed intake or external insulation was high, Experiment III), a greater body heat debt existed 2 h post-cooling. By reference to the results of the individual Experiments, it can be seen that where HC was high before rumen cooling, the increase in \dot{M} due to the cooling was low.

The body heat content buffer can be visualised diagrammatically (Figure 4.6). The complete buffer zone is defined by maximum and minimum body temperatures which are presumably a function of temperature regulatory 'set' points in the hypothalamus. The available buffer zone is dependent on the difference between the mean body temperature and the minimum body temperature. Mean body temperature depends on factors such as feed intake (level of heat production), insulation, ambient temperature and exercise. Also shown in this model is the effect of a single substantial drain on the HC buffer by, for example, a large meal of cold feed where the buffer is exceeded and a rise in heat production initiated. A comparable hypothetical situation is shown where the buffer is reduced on a number of occasions, but in small quantities so that at no time does body temperature fall below the minimum. In this latter case mean body

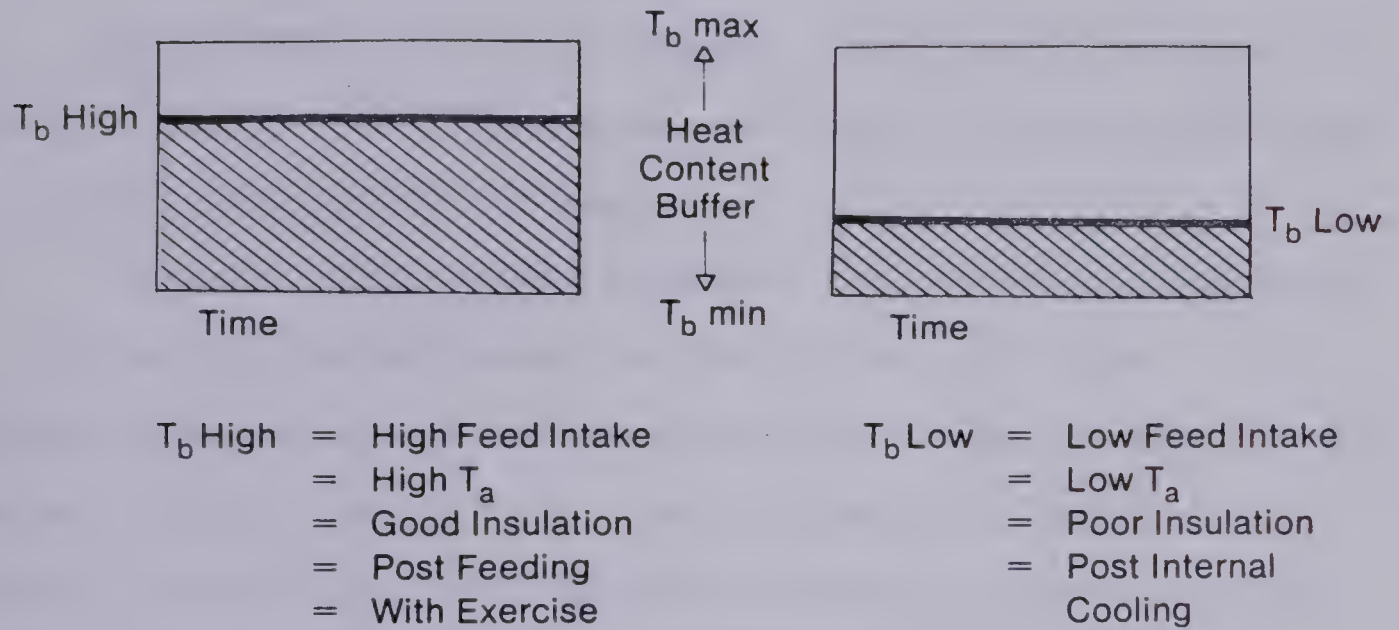
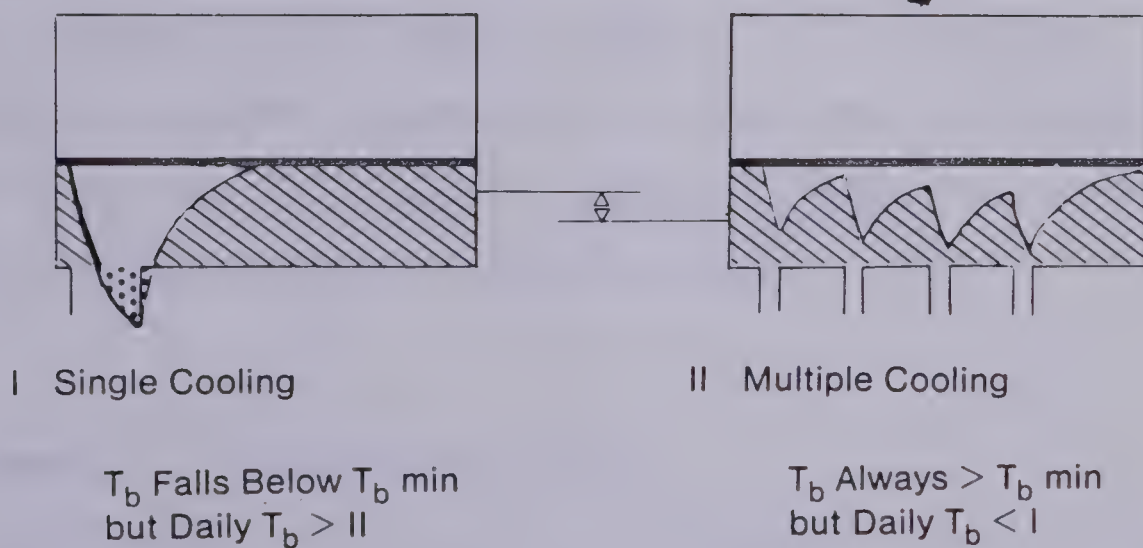
(a) Influence of T_b on Heat Content Buffer(b) Influence of Frequency of Cooling on T_b 

Figure 4.6 Model of body heat content buffer and influence of mean body temperature and body cooling on the body heat content buffer

temperature is lower over time than in the single cooling situation. Although the increase in energy expenditure has been avoided, the animal is likely to be at greater risk to further cooling for a longer time.

Such a heat buffer or thermal 'bank' would help explain some of the variable responses obtained to internal cooling in these and other experiments.

A closer study of the combined results from Experiments I, II and III could reveal critical levels of some temperatures or their combinations which might predict the physiological limits to the heat content buffer system in sheep. Such an approach has been taken in attempting to define the limits of heat and cold exposure in humans (Blockley, 1963; Hayward et al., 1977) and in a number of small mammalian species (see Stitt et al., 1974). However, at this stage in the present study it was considered necessary to gather information on the effects of continued exposure to internal cooling from cold feeds, rather than to predict the outcome of a single exposure.

4.5 Summary Experiments I-III

Rumen cooling by the direct infusion of water or by a cooling coil used to simulate the effect of ingesting cold feed and water elicited a number of responses in adult sheep.

Peripheral vaso-constriction was induced, presumably through the stimulation of rumen and deep body thermal

receptors. Sensible heat loss from the body would be reduced as a result of the vaso-constriction. The degree of peripheral vaso-constriction which occurred was

1. directly proportional to the quantity of rumen cooling (Experiment I), although this relationship must ultimately be limited by the minimum skin temperature.
2. dependent on the rate of rumen cooling. Faster rates of cooling caused a more rapid decline in skin and body temperatures (Experiment II).
3. influenced by the body temperature/heat content of the animal (Experiments I, III). Where pre-cooling body temperatures were high, a greater decline in skin temperatures occurred with cooling, although some drop in skin temperature did occur below thermoneutrality (Experiment III).

Skin temperature continued to decline *after* rumen cooling ceased (Experiment III). The relatively slow decline in skin temperature in response to the internal cooling limits the reduction in sensible heat loss.

Deep body (rectal) temperature also declined with rumen cooling (Experimented I, II and III) and represents a reduction in the total body heat content. With most of the rumen cooling treatments in these experiments, body temperatures were still below pre-cooling levels 2 h post-cooling. Presumably these animals would be more susceptible to further cooling either by the consumption of more cold food or by falling ambient temperatures.

Metabolic rate (M) increased in response to ruminal cooling (Experiments I and III) when body temperatures fell below a minimum. The increase in M was reduced, but not necessarily eliminated, when pre-cooling body temperatures were high (Experiment III). In this series of experiments the increase in M was never equivalent to more than 60% of the rumen cooling. The remainder of HW was expressed in a decline in body heat content and sensible heat loss.

Gradients of up to 6°C between the body and rumen core were established (Experiment I). The body-rumen temperature gradients were dependent on the quantity and rate of cooling (Experiments I and II), feeding during cooling (Experiment I) and pre-cooling physiological state (Experiments II and III). Heat would therefore flow from the body into the rumen in response to the reduced temperature in the rumen (Experiment I). Only 40 to 60% of the effective cooling of the rumen was recovered by the rumen from the body over the cooling period (Experiment I). The remainder of the rumen heat debt was recovered *after* cooling at a rate proportional to the temperature differential between the body and the rumen (Experiment II). The rumen acted as a thermal buffer between the animal and the effects of HW .

The heat of warming has a mass and temperature component either or both of which can vary. If the rumen is considered as a separate heat pool to the body, then it can be shown by theoretical calculation that the associative effects of a mass and temperature change should reduce the

temperature of the rumen pool less than the single effect of the temperature component. This effect was confirmed experimentally (Experiment I). It was concluded that the difference in animal response as a consequence of the method of cooling was unlikely to be of practical importance.

5. EXPERIMENT IV ENERGY EXPENDITURE OF SHEEP EATING TURNIPS

There is an absence of data for sheep on the energy expenditure associated with eating bulky, low dry matter feeds such as root crops. Drew (1967) suggested the energy expenditure may be high and a limiting factor to the performance of sheep on these crops.

Results from Experiment I indicated that the small increase in heat production associated with sporadic eating during a period of continuous rumen cooling did not substitute for a rise in heat production induced by the cooling. If the energy expenditure associated with eating root crops was high, then a greater potential may exist for substitution of the increase in heat production with eating for HW.

Adam et al. (1979) incorporated *sliced* turnips as one of five feeds in a study on the energy cost of eating in cattle, whereas under grazing conditions *whole* turnips are eaten. In severe winter climates such feed crops can freeze which could increase the energy expenditure associated with eating due to the hardness of the feed and the latent heat of fusion.

Experiment IV was designed to measure the energy expenditure associated with eating turnip bulbs in different physical forms by sheep and to compare the energy expenditure associated with eating turnips with that of more

conventional feeds.

5.0.1 Experimental Methods

5.0.1.1 Feeds

Four feed types were incorporated into a 4x4 Latin square design using 4 sheep. The feeds were

1. Whole Turnip Bulbs (WHOLE)

Whole turnip bulbs of a mean fresh weight of 0.9 kg were fed at an internal temperature of approximately 5°C. The turnips were fed in a wooden trough except during calorimetry trials when they were skewered together in a rigid upright position to simulate the grazing situation.

2. Sliced Turnips (SLICED)

Turnip bulbs (0.9 ± 0.3 kg fresh weight) were manually sliced into pieces with a mean fresh weight of 39 ± 17 g and fed loose in a wooden trough.

3. Frozen Sliced Turnips (FROZEN)

Sliced turnips were stored at -8°C for 12 to 24 h before feeding and fed as in (2).

4. Concentrate Pellet (RATION A)

The barley-alfalfa pellet was fed as a control feed.

At the conclusion of the main experiment long hay (LONG HAY) (brome grass mixture) was also used as a test feed.

5.0.1.2 Animals

Four 3.5 year old, woolly (8 to 10 cm fleece depth), Suffolk-cross, pregnant ewes with 6 fully erupted permanent incisors were trained over a two week period to eat all the feed types. The mean liveweight of the ewes was 77 ± 3 kg. During the training period all ewes were accustomed to, and fed in the ventilated hood and associated crate used for the calorimetric measurements.

Following the training period, each ewe was fed each test feed for 6 days before measurement of the energy expenditure associated with eating. During the pre-feeding period the ewes were held in individual 3x2 m pens and fed turnips ad lib or Ration A at $1000 \text{ g} \cdot \text{day}^{-1}$. Feed was offered once daily at 0900 h. Any feed not consumed was removed on the evening prior to a test day. The ewes were weighed once per week.

5.0.1.3 Measurements and Calculations

On each test day a sheep was fed the test ration at 0900 and 1500 h. The morning and afternoon trial involved the continuous measurement of oxygen consumption before (4x10 min periods), during (1 or 2x10 min periods) and after (4x10 min periods) eating. Only the morning measurement was made with the LONG HAY. All tests were made at an ambient temperature of 21 to 23°C.

Feed was placed in the hood under an expanded metal plate supported by the sides of the hood before each trial

began. The sheep did not appear to be excited by the presence of the feed. The expanded metal plate was raised for feeding and replaced after feeding by a rope to avoid opening the hood.

Air flow rate through the hood was $80 \text{ litres.min}^{-1}$ which gave a calorimeter response time of 2 min. To accommodate the small change in oxygen content of the extracted air (0.2 to 0.3 percentage units), a strip chart recorder with a variable full-scale voltage was used (Honeywell Controls Ltd., Model Electronic 19). The recorder was calibrated on the 10 mv scale and switched for the measurement period to the 2 mv full scale (15 cm) deflection equivalent to 0.8% oxygen.

Time spent eating was recorded. The sheep could be observed without disturbance through a mirror placed in front of the hood. Feed eaten was taken as the difference in weight of feed placed in the hood and that remaining at the end of the test period.

Oxygen consumption as a result of eating was calculated as the increase in oxygen consumption during eating above the mean of the two 10 min periods immediately before and after eating. Heat produced due to eating (total eating cost, kJ) and energy expenditure per min and per g of dry matter were calculated for each measurement by dividing the total cost of eating by the time spent eating and dry matter eaten.

The results were analysed as a Latin square with feed

type, sheep and periods as main fixed effects and morning and afternoon measurements as a split plot within the main design. The results for LONG HAY were not included in the analysis.

5.0.2 Results and Discussion

There was no statistically significant difference ($p < 0.05$) between the morning and afternoon trials so the pooled results are shown in Table 5.1.

The quantity of RATION A offered during a test was restricted below ad lib intake and was eaten very rapidly so the total time spent eating and the dry matter consumed was significantly ($p < 0.05$) different from all other feeds.

On an *as fed* basis turnips were consumed at approximately the same rate per min as RATION A while LONG HAY was consumed at one seventh of the rate. However when expressed as *dry matter* consumed per unit time, the turnips and hay were consumed at an equivalent rate which was one ninth that of RATION A. Similar differences in ingestion rate between these feeds consumed by cattle were observed by Adam et al. (1979).

No statistically significant differences were detected in any of the expressions of the relative cost of eating the various feed types but this may have been associated with the large variance of the total energy expenditure associated with eating SLICED and FROZEN turnips. When fed SLICED or FROZEN turnips, the sheep in some cases tended to

Table 5.1 Rate of eating and energy expenditure of sheep eating five feed types (Experiment IV)

	Feed types				
	RATION A	Turnip bulbs			LONG HAY ¹
		WHOLE	SLICED	FROZEN	
Time spent eating (min)	9.6a	15.7b	19.6b	21.9b	21.6
Feed eaten as fed (g)	560	790	810	920	160
dry matter (g)	483a	103b	105b	120b	133
as fed (g.min ⁻¹)	64.6	51.0	39.0	44.8	7.1
dry matter (g.min ⁻¹)	56.0a	6.5b	5.3b	5.9b	6.1
Total cost (kJ)	9.3a	25.1b	24.3b	30.2b	46.1
Cost per min (kJ.min ⁻¹)	0.99	1.59	1.22	1.39	2.13
Cost per kg feed (kJ.kg ⁻¹)	23	247	306	345	410
Cost per kg bodyweight per minute (kJ.kg ⁻¹ .min ⁻¹)	13.0	22.4	16.6	18.7	28.7
±SEM ²	0.9	2.6	0.9	3.1	1.3
kg dry matter (J.kg ⁻¹ .kg ⁻¹)	320	3470	4360	4710	5560
±SEM	66	300	1000	1615	840

¹ LONG HAY not part of the main experiment but additional data with the same sheep

² SEM Standard error of the mean for individual feeds

a,b,c,d means in rows followed by the same letter are not significantly different (p<0.05)

play with the slices as if undecided whether to take them into their mouths and chew them or to bite off pieces. On the other hand, when eating whole turnips, the sheep were generally very actively and fully involved in gouging pieces off the whole turnip bulb. This indecision when faced with SLICED and FROZEN turnips may have contributed to the high variance associated with these treatments.

A number of trends in the results deserve comment. The apparent energy expenditure per unit dry matter associated with eating turnips was approximately 10x that of eating RATION A but somewhat below (33%) that of LONG HAY. Adam et al. (1979) found the energy expenditure associated with eating sliced turnips by cattle was 7 times that for RATION A but above (60%) that for long hay.

The energy expenditure associated with eating the conventional feeds (RATION A and LONG HAY) are within the range recorded by others (Osuji, 1974; Osuji et al., 1975). The energy expenditure associated with eating turnips does not appear to be any higher than that reported for other low dry matter feeds such as cut grass (Graham, 1964a; Osuji et al., 1974) or for grazed pasture (Graham, 1964a; Holmes et al., 1978). Despite the *hard* nature of the turnip bulb the rate of ingestion (5 to 6 g dry matter.min⁻¹) was similar to that achieved for cut grass (4 to 7 g DM.min⁻¹).

No important differences in energy expenditure associated with eating turnips in the three different forms were measured. However when a comparison between the

pattern of oxygen consumption of sheep eating SLICED and FROZEN is made (Figure 5.1), the absolute increase in oxygen consumption was much greater for the FROZEN turnips. This greater increase represented energy expenditure associated with eating, plus presumably an increment due to the cooling effect of the FROZEN turnips. When FROZEN turnips were eaten the cumulative increase in oxygen consumption *above* SLICED (the increase due to heat of warming) was 196% greater than the increase in oxygen consumption due to eating SLICED turnips.

In this example the method used to calculate energy expenditure associated with eating (the shaded area in Figure 5.1) gives similar areas, and thus energy expenditure associated with eating, for both SLICED and FROZEN turnips. Whether the same conclusion would be reached in other situations where both eating and HW are contributing to the increase in M during feeding is not known.

5.0.3 Summary Experiment IV

The energy expenditure associated with eating a gram of dry matter as turnip bulbs by sheep is seven to ten times that associated with eating a concentrate pellet but similar to that associated with other bulky feeds such as hay and grass. It is unlikely then, that a high cost of eating per se is limiting the performance of sheep fed root crops. There would appear to be no justification for slicing turnips in an attempt to reduce the energy expenditure

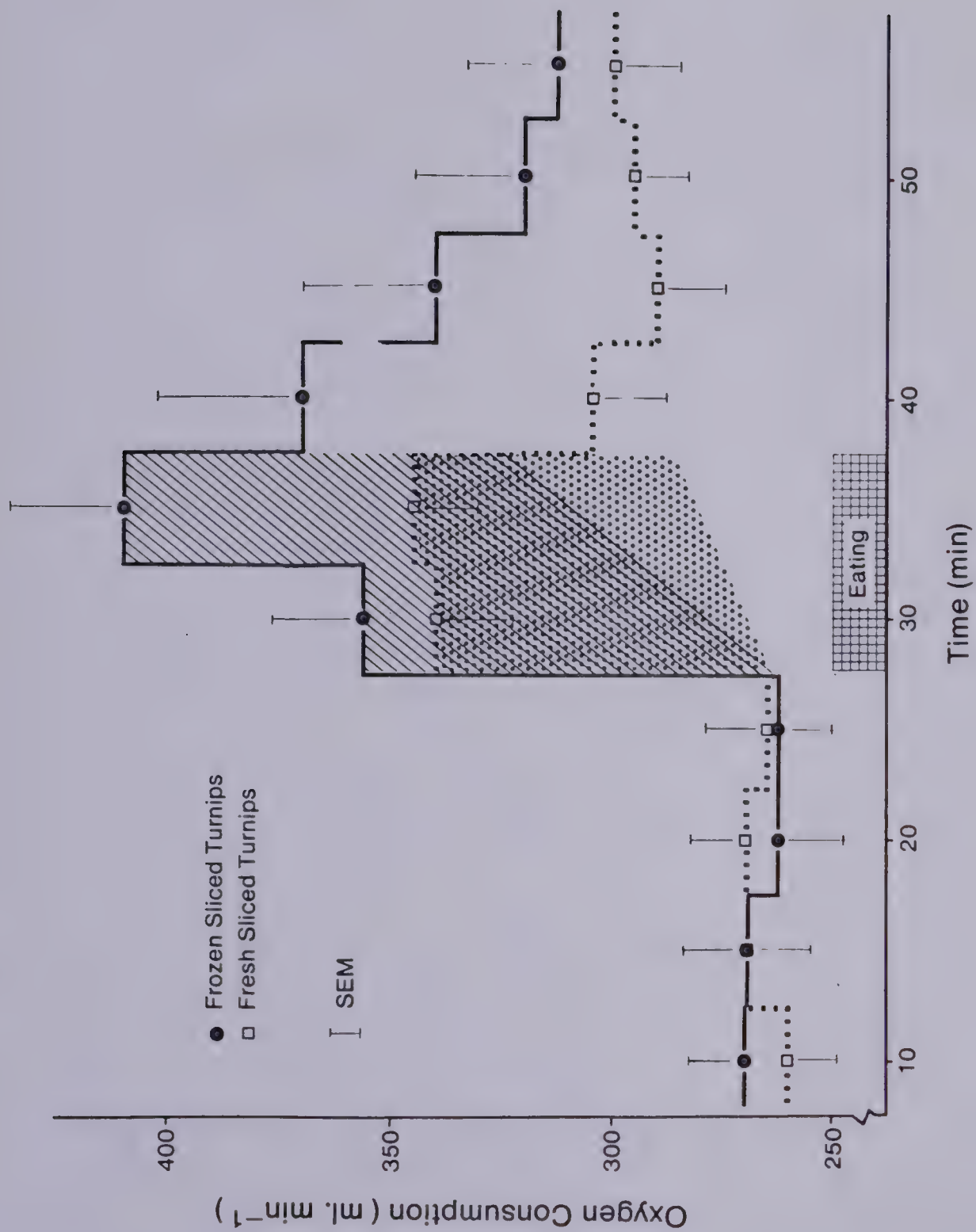


Figure 5.1 Oxygen consumption of sheep before, during and after eating fresh SLICED (broken line) or FROZEN sliced (solid line) turnips (Experiment IV)

associated with eating them. Care should be taken in interpreting the energy expenditure associated with eating in experiments where the increase in heat production during eating could be a function of both eating and warming the food.

6. EXPERIMENTS V, VI and VII CONSUMPTION OF HIGH MOISTURE FEED BY CATTLE

In Experiments I, II and III rumen cooling treatments were allocated in random order on a *daily* basis. Under field conditions, feed may be consumed at a similar temperature repeatedly over a period of days or weeks and cumulative effects of the heat of warming may develop in the animal. The impact of different levels of heat of warming (HW) imposed on cattle twice daily for two weeks was examined in Experiment V.

As cold feed is eaten some cooling might be expected to occur in the mouth rather than exclusively in the rumen as simulated in Experiments I, II and III. The response to cooling via the rumen was compared with the consumption of cold feed (Experiment VI) and estimates were made in Experiment V of the proportion of cooling occurring in the mouth.

The results of field trials indicate that partial substitution (20 to 30% of dry matter intake) of a high moisture ration with a high dry matter, low quality roughage was beneficial to animal performance (see Nicol and Barry, 1980). In theory such a substitution should reduce energy intake and the heat of warming and possibly increase heat production from rumen fermentation. Experiment V incorporated a treatment in which such a feed substitution

was made. If a substitution effect was dependent on fermentation heat, then the order in which the two parts of the ration were fed might be important. Experiment VII addresses this question.

Cattle were chosen as the experimental species in these experiments since comparable data on the effects of HW on cattle other than young calves were required and because cattle had some technical advantages in these experiments.

6.1 Experiment V Responses of cattle fed turnips of various temperatures

Four feeding treatments, incorporating different levels of HW were compared in a Latin Square designed study involving 4 steers.

6.1.1 Experimental Methods

6.1.1.1 Feeding Treatments

The four treatments were:

1. Warm Turnips (WARM)

Whole turnip bulbs (15 kg total fresh weight, 0.9 ± 0.3 kg per bulb) fed at a turnip temperature of 27°C .

2. Cold Turnips (COLD)

Fifteen kg fresh whole turnip bulbs fed at a temperature of 2°C .

3. Turnips plus Hay (TURHAY)

Whole COLD turnip bulbs fed as 70% of dry matter intake with the balance as chopped hay (10 kg fresh turnip bulbs and 1 kg hay). The turnips were fed first followed immediately by the hay.

4. Frozen Turnips (FROZEN)

Fifteen kg sliced turnip bulbs (mean fresh weight of pieces 57 ± 18 g) and stored at -8°C for 18 to 24 h before feeding.

All rations were fed twice daily at 0830 and 1700 h. The four treatments represented a heat of warming per meal of 0.70, 1.54, 2.18 and 6.00 MJ for the WARM, TURHAY, COLD and FROZEN treatments respectively. All rations were designed to provide the same digestible dry matter intake.

6.1.1.2 Animals

Four 2.5 year old cross-bred beef steers (mean liveweight 406 ± 5 kg) were rumen fistulated two months prior to the experiments by the method of Hecker (1974). The steers had been used in previous experiments (Adam et al., 1979) and were accustomed to eating turnips and to gaseous exchange measurements.

Each experimental period was 14 days but space limitations precluded holding more than two steers in the 10°C environmental room. For days 1 to 7 of each period the steers were held in individual 3x3 m pens in a holding building where the ambient temperature ranged from 9 to 15°C. From day 8 to 14 of the period the steers were held in metabolic crates in the 10°C room.

Each steer was fitted with ear, leg and trunk skin and an external jugular vein thermocouple on day 8. The cattle were weighed on days 8 and 14. Total faecal output was collected from day 8 to 13 inclusive.

6.1.1.3 Measurements and Analysis

Feed Treatments

Measurements were made on each steer on one morning (0830 to 1230 h) and one afternoon (1430 to 1730 h) on days 10 and 12 or 11 and 13.

Oxygen consumption (System A), ear, leg and trunk skin temperature, rectal and jugular temperature and rumen temperature (2 thermocouples through the rumen cannula) were measured continuously over a 1 h pre-feeding period, a 1 h feeding period and 2 h (am) or 1 h (pm) recovery period. Feed was introduced and removed from the hood by a drawer without interference to the gaseous exchange measurements.

Method of Mixtures

Method of mixtures calorimetry was used to measure the temperature of boli collected from the steers, pieces of turnip, snow, ice and *pseudo* turnip (85% ice, 15% turnip dry matter). Tared Dewar flasks (500ml) of known heat capacity (80 to 90 J. $^{\circ}\text{C}^{-1}$) containing a known weight of water (± 1 g) of a known temperature (± 0.1 $^{\circ}\text{C}$, Bailey Instruments Inc., Model BAT 8) were used. The unknown mass at unknown temperature was added to the flask and the flask plus contents reweighed. The equilibrium temperature of the mixture was recorded.

Bolus Size and Temperature

During days 10 to 13 inclusive of each experimental period and when the measurements associated with feed consumption were not being made, the following additional

data were gathered. The rumen of each steer while on the WARM, COLD and FROZEN treatments was emptied prior to the morning feeding (15 h post-feeding) and the contents weighed. The steer was then fed and two boli were caught on separate occasions in a gloved hand at the cardia. Each bolus was immediately transferred to a tared, 500 ml Dewar flask to measure the mean temperature of the bolus as it reached the rumen.

The bolus:water mixture was dried (24 h at 70°C) to give the total dry matter in the bolus. The dry matter percentage of the turnip before feeding was known (13%) and thus the contribution of fresh turnip and saliva to total bolus weight was calculated. The heat gained by the bolus before reaching the rumen was calculated by assuming that saliva was secreted at body temperature.

Statistical Analysis

Statistical analysis was as a 4x4 Latin square with feed treatments, steers and periods as main fixed sources of variance. The am and pm comparison was treated as a split-plot within the main experiment and the hourly time periods as a further split.

6.1.2 Results and Discussion

6.1.2.1 Change in turnip temperature during eating

The temperature of the WARM turnips fell by 3.5°C and that of the COLD turnips increased by 3.3°C as they lay in

the trough over the 1 h eating period. About 50% of the increase in temperature of the COLD turnips could be attributed to the presence of the steer, presumably due to exhaled warm air. The temperature at which the turnips were actually consumed was adjusted for this change before calculating the heat of warming. The FROZEN turnips remained frozen during the eating period.

6.1.2.2 "Effective" temperature of turnips

The temperature of the turnips calculated from the calorimetric method of mixtures has been defined as the "effective" temperature (ET). ET is the temperature of the frozen turnips with no consideration of the latent heat of fusion, simply the change in heat content of the Dewar flask by adding the turnips to the water expressed per g of turnip. ET temperatures and the equivalent probed temperature for calorimetric runs on turnips at a range of temperatures are shown in Figure 6.1. Probed temperature was measured by a copper-constantan thermocouple or platinum resistance thermometer probe pushed into the turnip.

At temperatures above 0°C the probed turnip temperature and the temperature calculated by the method of mixtures were similar and validate the use of a specific heat of approximately 1.0 for fresh turnips. Below 0°C, snow, ice and a *pseudo* turnip of 85% ice and 15% dried turnip gave 'effective' temperatures close to theoretical values. Frozen turnips exhibited a progressive crystallisation; an

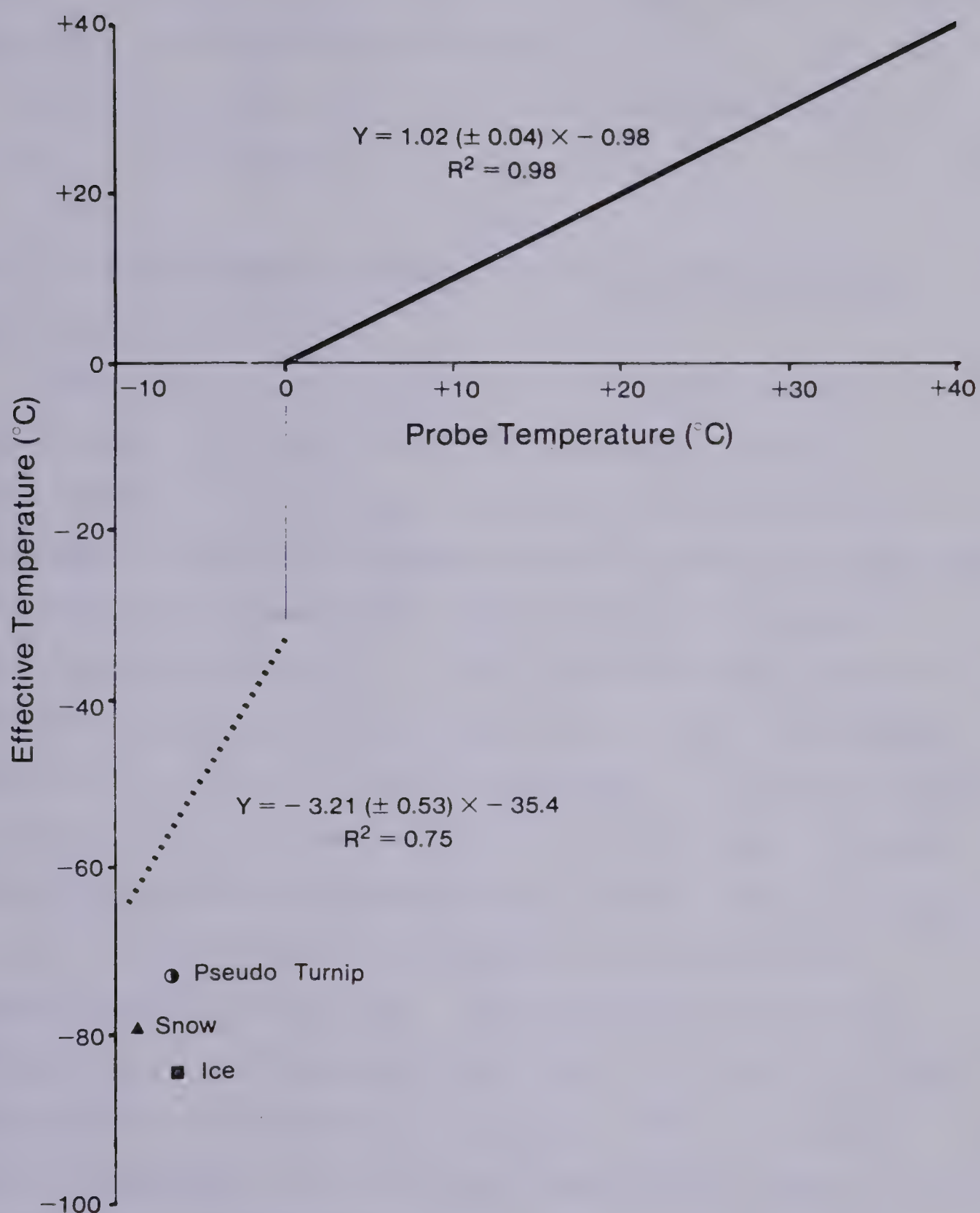


Figure 6.1 Relationship of effective turnip temperature with probed turnip temperature (Experiment V) (solid line above 0°C; broken line below 0°C) Tests with snow, ice and pseudo-turnip (85% ice, 15% turnip dry matter) are also shown

effect of the soluble plant components (Fennema et al., 1973) with approximately 50% crystal formation at 0°C and maximum crystallisation predicted to occur at -11°C. The frozen turnips were physically harder (more difficult to break) at -8°C than at 0°C.

6.1.2.3 Feed Intake and Heat of Warming Achieved during Calorimetric Trials

When steers were not involved in a calorimetric measurement all feed offered was consumed. During measurement trials feed was removed at the end of Period II and some variation in intake occurred between treatments due to steers not finishing the ration within the one hour feeding period (Table 6.1). The rate of eating turnips was similar to that observed by Adam et al. (1979) and showed that cattle as well as sheep (Experiment IV) consumed whole, sliced, fresh or frozen turnips at similar rates. The mean percentage dry matter digestibility of the turnip bulbs was $86.6 \pm 1.1\%$ and was not significantly influenced by the temperature of the turnips. The percentage dry matter digestibility of the mixed ration was $76.3 \pm 0.9\%$. The mean pre-feeding rumen volume of steers on complete turnip rations was 30.4 ± 2.4 litres which was not influenced by the temperature of the turnips.

6.1.2.4 Warming in the Mouth

The weight and temperature of the boli collected from

Table 6.1 Feed intake and heat of warming achieved during trials with steers (Experiment V)

	Feeding treatment			
	WARM	TURHAY	COLD	FROZEN
Feed consumed (fresh wt)				
turnips (kg)	12.6	10.0	12.9	13.2
hay (kg)	-	1.0	-	
Digestible dry matter intake (kg)				
on test day ¹	1.39	1.63	1.42	1.45
on full intake	1.65	1.63	1.65	1.65
Rate of eating (g dry matter.min ⁻¹)				
turnips	210	220	215	220
hay	-	67	-	-
Turnip temperature (°C)	26.7	2.1	2.1	-7.2
±SEM	0.52	0.52	0.52	0.55
Heat of warming (MJ)				
on test day	0.62	1.54	1.96	5.27
on full intake	0.70	1.54	2.18	6.00
Cooling per DDMI ² (MJ.kg DDMI)	0.39	0.94	1.32	3.63

Dry matter digestibility of turnips = 86.6±1.1% (see text)
mixed ration = 76.3±1.0%

Body temperature = 38.5°C, Effective temperature
of frozen turnips = -57°C

¹ on test day = mean feed intake during calorimetric runs
on full intake = feed intake as designed

² DDMI = Digestible dry matter intake

the steers as they consumed turnips at various temperatures is shown in Table 6.2.

Table 6.2 The temperature, weight and saliva content of boli from steers consuming turnips of various temperatures (Experiment V)

	Turnip temperature			±SEM
	WARM	COLD	FROZEN	
Temperature (°C)				
turnips as fed	27.9a	2.0b	-8.5c ²	0.19
bolus in rumen ¹	29.3a	18.5b	-18.3c	0.11
turnip in rumen ¹	22.0a	3.9b	-55.0c	0.7
Wt. of bolus (g)	72	86	98	8
Saliva in bolus % by weight	44.8	42.5	49.2	3.9

¹ Effective temperature as calculated from the calorimetric method described in methods.

² Equivalent effective temperature -65°C

a,b,c,d means in rows followed by the same letter are not significantly different (p<0.05)

Calculations from these data show that 6.4 and 10.6% of the total heat required to warm the turnips to body temperature had been contributed before the rumen in the COLD and FROZEN turnips respectively. With WARM turnips, a heat loss equivalent to 1% of the total heat content of the bolus occurred in the mouth and oesophagus. Since the WARM turnips were fed at 17°C above T_a , heat could be lost to the environment as chewing took place. If correction is made for the apparent heat loss in the mouth then 12.2 and 18.4% of the total heat of warming could be attributed to the

mouth with COLD and FROZEN treatments respectively.

With a rate of eating of $216 \text{ g} \cdot \text{min}^{-1}$ and mean weight of turnip in a bolus of 46 g, 4.7 boli would be swallowed each minute. For the COLD and FROZEN turnip boli it was estimated that 44 and 146 W respectively entered a bolus while in the mouth. This rate of heat flow is equivalent to 7 and 28% of the total heat production of the steers.

A particle size distribution analysis of boli collected from the steers indicated that about 33% of the total bolus dry matter consisted of turnip pieces with a dry weight of over 1 g. The relatively large size of the turnip pieces presumably results in a small surface area per unit mass which may reduce the rate of heat transfer to the bolus both in the mouth and in the rumen. If the turnips were chewed into smaller particles, such as would occur with fresh forage a faster dissipation of the cooling might occur and rumen temperature might have fallen to a greater extent. The large size of the pieces may also have implications to rate of fermentation and rumen turnover as indices of ruminal digestion.

6.1.2.5 Body and Rumen Temperatures

Feeding treatment significantly influenced rectal, jugular, ear skin and rumen core temperature (Table 6.3). The lowest level of HW (0.62 MJ per meal) with the WARM turnips was insufficient to markedly reduce the rise in body temperature associated with eating in cattle (Ingram and

Table 6.3 Heat of warming treatment by period interaction means for rectal, jugular, ear skin, mean body and rumen core temperature (Experiment V)

	Period				
	I	II	III	IV	±SEM
Rectal temperature (°C)					
WARM	38.0 ^{ae}	38.2 ^{abef}	38.4 ^{abe}	38.5 ^{be}	0.03
TURHAY	38.0 ^{ae}	37.9 ^{af}	38.2 ^{ae}	38.3 ^{aef}	
COLD	38.6 ^{af}	38.6 ^{ae}	38.6 ^{ae}	38.6 ^{ae}	
FROZEN	38.3 ^{aef}	37.8 ^{bf}	37.5 ^{bf}	37.9 ^{abf}	
Jugular temperature (°C)					
WARM	37.7 ^{aef}	38.2 ^{bf}	37.9 ^{abef}	37.8 ^{abe}	0.03
TURHAY	37.3 ^{ae}	37.4 ^{ae}	37.5 ^{af}	37.6 ^{ae}	
COLD	38.2 ^{ag}	38.0 ^{af}	38.1 ^{ae}	38.1 ^{ae}	
FROZEN	37.9 ^{afg}	37.0 ^{be}	37.0 ^{bg}	38.1 ^{abe}	
Ear skin temperature (°C)					
WARM	27.1 ^{ae}	26.9 ^{ae}	32.5 ^{ae}	33.1 ^{ae}	0.5
TURHAY	27.6 ^{ae}	25.2 ^{ae}	26.2 ^{aef}	30.1 ^{aef}	
COLD	32.7 ^{ae}	26.5 ^{be}	31.4 ^{abe}	33.2 ^{ae}	
FROZEN	28.4 ^{ae}	25.4 ^{ae}	23.0 ^{af}	24.2 ^{af}	
Mean body temperature (°C)					
WARM	34.1 ^{ae}	34.2 ^{ae}	34.5 ^{ae}	34.8 ^{ae}	0.3
TURHAY	34.6 ^{ae}	34.2 ^{ae}	34.4 ^{ae}	34.6 ^{ae}	
COLD	34.8 ^{ae}	34.7 ^{ae}	34.9 ^{ae}	34.9 ^{ae}	
FROZEN	35.1 ^{ae}	34.2 ^{abe}	33.8 ^{be}	33.9 ^{be}	
Rumen core temperature (°C)					
WARM	38.2 ^{ae}	38.6 ^{ae}	39.2 ^{abe}	39.6 ^{be}	0.15
TURHAY	38.2 ^{abe}	37.0 ^{cf}	38.1 ^{bce}	39.4 ^{ae}	
COLD	38.9 ^{ae}	36.6 ^{bf}	38.2 ^{ae}	39.3 ^{ae}	
FROZEN	38.3 ^{ae}	31.4 ^{cg}	34.4 ^{bf}	37.7 ^{af}	

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

Whittow, 1962). The intermediate levels of HW (TURHAY and COLD treatments) caused body temperatures to decline but recovery was complete by Period IV. A large decline in body temperatures occurred when FROZEN turnips were consumed and little recovery had taken place two hours after cooling stopped.

Rumen temperature was significantly ($p < 0.05$) higher by 0.6°C before feeding in the afternoon than before feeding in the morning. Rectal and jugular temperature also showed this trend (0.2 and 0.1°C respectively) but these slightly higher temperatures did not appear to reduce the impact of HW in the afternoon. There was no interaction between feed treatment and am or pm measurements, indicating no differential carry-over effect from the morning and afternoon measurements.

Pre-cooling body temperatures in the morning were not obviously influenced by the previous 10 days of differential HW treatment. There was no particular evidence that the TURHAY (turnips plus hay) induced any less of a decline in body or rumen temperatures than the level of HW involved would suggest.

6.1.2.6 Oxygen Consumption

Oxygen consumption during Periods II and III was significantly ($p < 0.05$) above the other treatments for FROZEN turnips, but only in Period II for the COLD treatment (Table 6.4). In the latter part of Period II and for about half of

Table 6.4 Heat of warming treatment by period interaction means for oxygen consumption (litres.min⁻¹) (Experiment V)

	Period			
	I	II	III	IV
WARM	1.21 ae	1.70 be	1.49 abe	1.36 abe
TURHAY	1.27 ae	1.76 be	1.48 abe	1.50 abe
COLD	1.30 ae	1.83 be	1.66 $abef$	1.58 abe
FROZEN	1.30 ae	2.26 bf	2.09 bf	1.57 ae

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

Table 6.5 Heat production of steers relative to the heat of warming (Experiment V)

	Feed Treatment			
	WARM	TURHAY	COLD	FROZEN
Heat of warming (MJ) total HW per meal (1 hour)	0.62	1.54	1.96	5.27
Heat production (MJ) total M during the feeding hour	2.17	2.20	2.25	2.85
increase in M during feeding over Period I	0.59	0.56	0.67	1.24
cumulative increase in M over 3 h (Periods II, III, IV)	1.13	1.14	1.43	2.48

Period III steers on the FROZEN treatment shivered. In most cases shivering did not stop the steers eating.

A slight trend existed towards higher pre-feeding oxygen consumption in the morning for steers on the FROZEN turnips (FROZEN treatment 7% above WARM). However, when am and pm pre-feeding data were combined this trend was no longer evident. Combined am and pm pre-cooling oxygen consumption was 1.30, 1.33, 1.28 and 1.31 litres.min⁻¹ for the WARM, TURHAY, COLD and FROZEN treatments respectively. Thus even with a continuous period (10 to 13 days) of different levels of HW, any increase in *M* induced by the cooling was temporary over the feeding period and 2 to 3 hours post-feeding.

The heat production of the steers over the feeding period and the accumulated increase in *M* over pre-cooling levels for the time after cooling relative to HW is shown in Table 6.5 . Oxygen consumption showed an increase over pre-feeding values of 38, 37, 48 and 84% during feeding (Period II) for the WARM, TURHAY, COLD and FROZEN treatments respectively. The increase of 0.59 to 0.67 MJ could be accounted for solely by the energy expenditure associated with eating turnips (Adam et al., 1979). The increase in *M* during feeding was equivalent to 95, 35, 34 and 23% of the total HW in the WARM, TURHAY, COLD and FROZEN treatments.

Oxygen consumption over the measured 7 h (am plus pm) was extrapolated to 24 h total oxygen consumption using values of 1.31, 1.34, 1.36 and 1.36 litres.min⁻¹ (the

weighted mean of a progressive decline from post-feeding afternoon to pre-feeding morning oxygen consumption) for the 13 h period following the pm treatment through to the am pre-feeding period. Daily heat production was calculated from oxygen consumption to be 39.1, 40.0, 40.5, and 43.1 MJ for the WARM, TURHAY, COLD and FROZEN respectively. The increase in daily M over WARM was 2.8, 3.6 and 10.4% for the TURHAY, COLD and FROZEN treatments. While these differences are not large, they are similar to differences in daily energy expenditure associated with consuming feeds of different physical forms, a topic which has received considerable research effort compared with the cost of warming the feed.

At the higher levels of HW, much of the HW is unaccounted for by an increase in M and is absorbed as a decline in H and HC . This conclusion is similar to earlier work in this series (Experiments I, II and III) and to the studies of Holmes (1970, 1971b).

6.2 Experiment VI Comparison of cooling by the mouth or the rumen

Experiment VI compared the effects of the same quantity and rate of HW caused either by eating cold turnips or predominantly by cooling the rumen.

6.2.1 Design and Measurements

The experiment was made on steers receiving the COLD treatment in Experiment V. On a morning prior to, or afternoon following a measurement in Experiment V the steers were offered 15.0 kg of WARM turnips and the rumen was cooled by 1.4 MJ using the rumen cooling coil, giving a total cooling equivalent to the consumption of COLD turnips. Approximately 70% of the cooling was via the rumen cooling coil and the remainder from feed consumed. A comparison of the results obtained from the two sites of cooling was made using the same measurements as in Experiment V. The data were analysed by analysis of variance of the randomised split plot design with all interactions with steers used as the error variance.

6.2.2 Results and Discussion

The only significant difference measured between the two sites of cooling was a lower rumen temperature when the coil was used (Table 6.6). *Tru* was lower in Periods II, III and IV.

Table 6.6 Mouth vs rumen cooling treatment by period
interaction means for rumen temperature ($^{\circ}\text{C}$)
(Experiment VI)

	Period			
	I	II	III	IV
Turnips (2.1°C)	39.2 ae	36.7 ce	38.2 be	39.4 ae
Turnips (26.7°C) plus 1.4 MJ cooling (by COIL)	39.0 ae	35.4 cf	37.3 bf	38.6 af
<p>a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)</p> <p>e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)</p>				

Due to the presence of the coil in the rumen, turnip intake was reduced from 12.9 to 9.6 kg per meal presumably due to bulk limitation to intake (see Baile and Forbes, 1974). A calculation similar to that when the COIL and INFUSION methods of cooling were compared in Experiment I, but using bolus temperatures and saliva:turnip ratios from Experiment V was made. Due to the difference in turnip intake, a 1.7°C difference could be anticipated between treatments with the rumen cooling showing the lower temperature. A part of the additional 1.7°C drop in Tru was because the supplementary cooling by the coil was designed on a basis of the COLD turnip intake and thus the total cooling by coil plus WARM turnips was too high (6%) for the lower turnip intake.

On the basis of the relatively small percentage of the heat of warming which occurred in the mouth (Experiment V) and the lack of important differences between the HW by mouth or rumen in this experiment, rumen cooling would appear to be an acceptable experimental model for studies on the heat of warming.

6.3 Experiment VII Turnips fed before or after hay

The order in which a mixed ration of 10 kg COLD and 1 kg of chopped hay was fed was compared in this Experiment.

6.3.1 Experimental Design and Measurements

The experiment was made on steers during the TURHAY treatment in Experiment V. On a morning prior to, or afternoon following, a trial on the TURHAY treatment the steers were fed hay prior to turnips, whereas in a TURHAY measurement turnips were fed first. A comparison of the influence of order of feeding the two feeds on changes in body temperatures, rumen temperature and oxygen consumption was made. Similar measurements were made as in Experiment V and the data were analysed as for Experiment VI.

6.3.2 Results and Discussion

By feeding turnips before hay, rumen temperature was lower in Period II (Table 6.7) than if hay was fed first. This interaction is shown more explicitly in Figure 6.2. The difference due to the order of feeding on rumen temperature was an alteration in phase of the time course change in rumen temperature rather than a marked influence on the amplitude of the change. There was no other significant effect of order of feeding.

There is little evidence from this experiment that the order of feeding the high moisture feed in a mixed ration

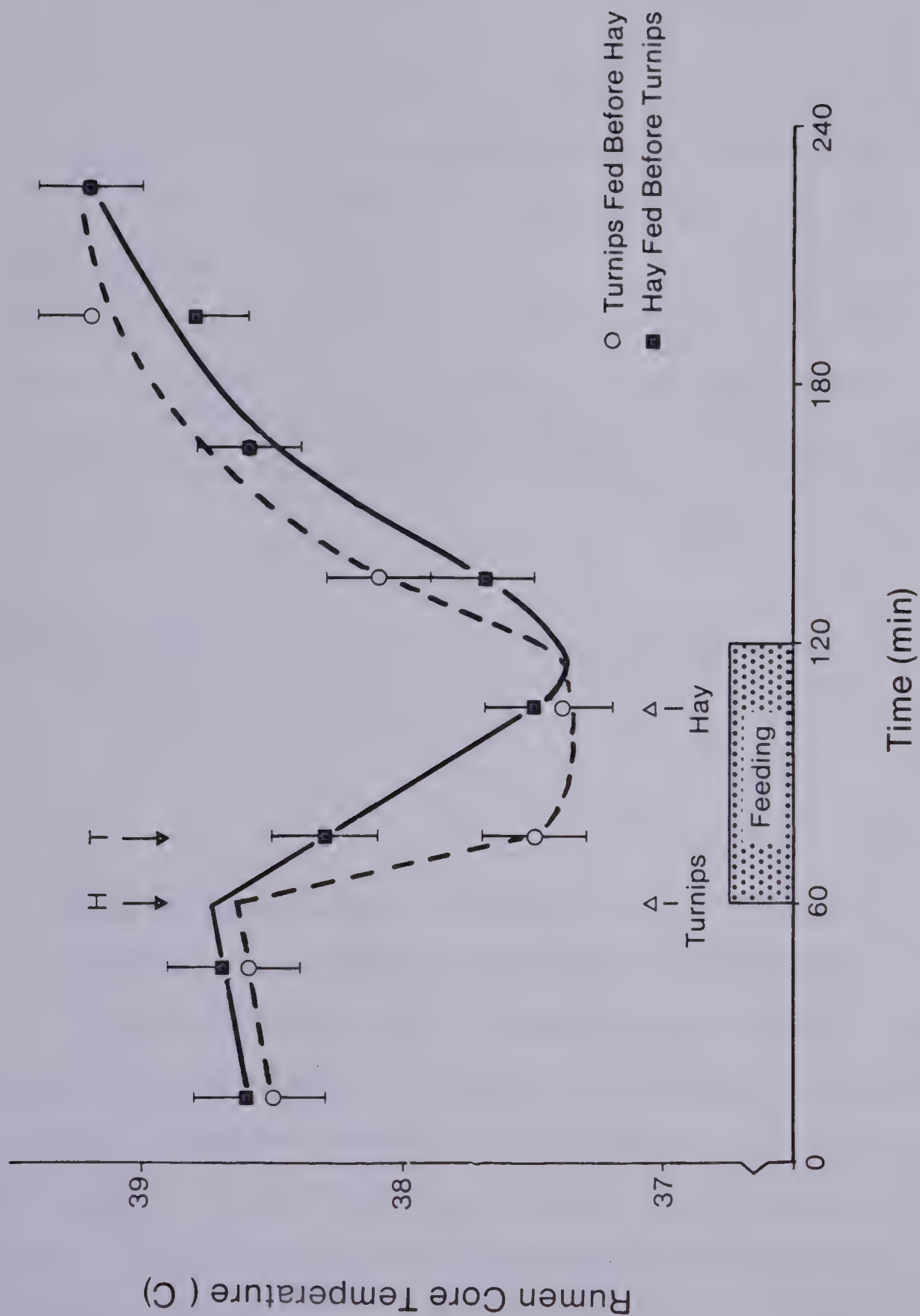


Figure 6.2 Effect of feeding turnips before hay (broken line), or hay before turnips (solid line) on rumen temperature of steers (Experiment VII)

Table 6.7 Order of feeding treatment by period interaction means for rumen core temperature ($^{\circ}\text{C}$) (Experiment VII)

	Period				$\pm\text{SEM}$
	I	II	III	IV	
TURNIPS before HAY	38.6 ae	37.5 be	38.4 ae	39.2 ce	0.14
HAY before TURNIPS	38.7 ae	38.2 af	38.2 ae	39.0 be	

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

has any important effect on the response to the cooling.

6.4 General Discussion Experiments V, VI and VII

6.4.0.1 Heat and Mass Transfers during Eating

From data collected in Experiments V, VI and VII it was possible to estimate on a theoretical basis the various heat and mass transfers that took place during feeding. A number of assumptions are necessary but the conclusions give an indication of the relative importance of the various heat and mass transfers.

The following data from Experiment V were used.

1. The mass and temperature of the feed consumed by steers during the calorimetric runs.
2. The mass and temperature of the rumen contents, before and after the morning feeding period.
3. The computed mean body temperature of the steers before and after feeding (as described in General Methods).
4. The mass of saliva leaving the body and entering the rumen, estimated from the saliva:turnip ratios in the boli collected. Since feeding was continuous over the eating period, it was assumed that all saliva entering the rumen was associated with boli.
5. The heat production of the steers before and during feeding.
6. Heat flows from the body to the mouth, extrapolated from the results with individual boli.

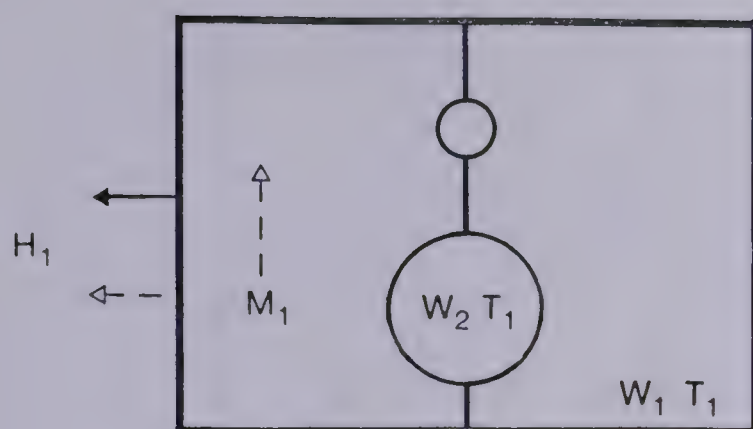
The following assumptions were made:

1. Before the morning feeding, thermal equilibrium existed between the rumen and the body and between the body and the environment, eg. $T_r = T_{ru}$ and $M = H$.
2. Mass lost from the rumen during feeding was equal to the pre-feeding mass of the rumen contents plus additional saliva and feed, less the mass of the rumen contents at the end of the feeding period. No distinction was made between the mass leaving as

- digesta or as water efflux across the rumen wall.
3. The mass leaving the rumen pool did so at the mean temperature of the rumen contents and that this mass would equilibrate with body temperature.
 4. That evaporative (E) heat loss was minimal (17 W.m^{-2} Blaxter and Wainman, 1961) and the mass loss associated with E (120 g.h^{-1}) was insignificant in the mass transfers involved and could be ignored.
 5. The mass loss from the body as urine and faeces would not be greater than $1\% \text{ body weight.h}^{-1}$ which would have little impact on the calculation of body heat content.

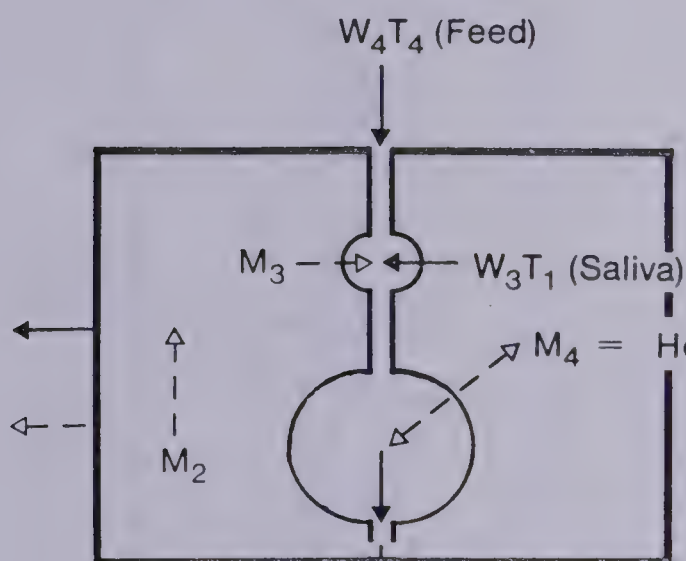
The total heat gained or lost by the rumen was calculated. Heat flows were calculated from a base of 0°C . By reference to the temperature gradient between the body core and the rumen, the change in rumen heat content was mathematically apportioned to heat produced in the rumen from fermentation and that transferred with the body. Finally, since the change in total body heat content was estimated from the change in mean body temperature, some indication of change in heat loss to the environment could be made. The model proposed for this analysis is shown in Figure 6.3.

The results of such a heat transfer balance for the steers in Experiment V is shown in Table 6.8 for the am



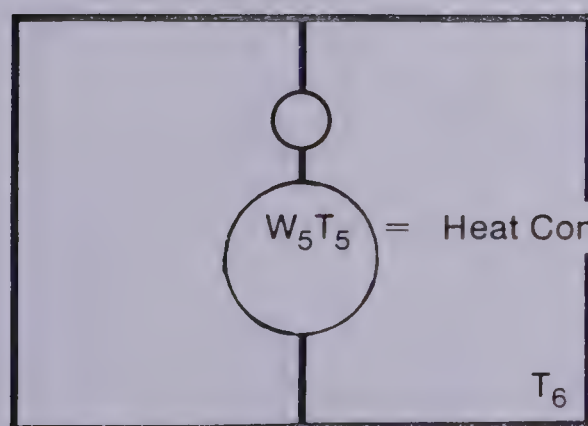
(1) Steady State
Pre-Feeding

$W_2 T_1$ = Rumen Heat Content
 $W_1 T_1$ = Body Heat Content



(2) During Feeding

Outflow (Rumen)
 $= (W_5 - W_2 + W_4 + W_3)$
 $\times (T_1 + T_5) \quad 2$



(3) Post-Feeding

— Mass + Heat Flow
 - - - Heat Flow

Figure 6.3 Mass and heat transfers between the body, the rumen and the environment during feeding (Experiment V)

Table 6.8 Heat transfer ($\text{MJ}\cdot\text{h}^{-1}$) between the body and rumen during eating in steers fed turnips at 4 temperatures (Experiment V)

Site of heat transfer	Feed treatments							
	WARM turnips		70% COLD turnips		COLD turnips		FROZEN turnips	
	body	rumen	body	rumen	body	rumen	body	rumen
Pre-feeding steady state								
metabolic rate (M)	+1.48	--	+1.56	--	+1.59	--	+1.59	-
heat loss (H)	-1.48	--	-1.56	--	-1.59	--	-1.59	-
During feeding								
(1) Heat and mass								
feed	--	+1.41	--	+0.16	--	+0.11	--	-3.15
saliva	-1.61	+1.61	-1.76	-1.76	-1.65	+1.65	-1.69	+1.69
rumen outflow	+1.61	-1.61	+1.56	-1.56	+1.58	-1.58	+1.41	-1.41
(2) Heat								
body to mouth	--	--	-0.09	+0.09	-0.11	+0.11	-0.53	+0.53
body to rumen	+0.09	-0.09	-0.47	+0.47	-0.66	+0.66	-2.10	+2.10
M (rumen)	--	+0.80	--	+0.80	--	+0.80	--	+0.80
M (body)	+2.08	--	+2.16	--	+2.24	--	+2.77	--
change in body								
heat content (HC)	+0.39		-0.63		-0.63		-1.41	
Predicted change								
in heat loss (H)	-1.78		-1.88		-1.40		-1.27	

feeding measurements. Changes in mass have been omitted from the table because no major net change in body mass occurred. Loss in body mass to the rumen as saliva (10 to 11 kg) was almost equal to the gain in mass moving from the rumen during feeding which was calculated as 10 kg based on before and after feeding rumen volumes. The following points may be noted:-

1. Unless rumen temperature decreased by more than 5°C during cooling/feeding, the net gain in heat by the rumen from saliva was offset by the loss in heat through rumen contents moving out of the rumen to the body.
2. Heat flow from the body to the mouth was small relative to other heat flows except for the FROZEN treatment where it was 0.53 MJ.
3. Heat released in the rumen during the feeding hour was greater than the heat flow from the body to the rumen in all but the FROZEN treatment. The 0.80 MJ of heat generated in the rumen represented the heat gained by the rumen from fermentation if there had been no temperature differential between rumen and rectal temperatures and represented approximately 3.5% of the digestible energy intake over the feeding period.
4. Heat flow into the rumen of greater than about 0.50 MJ over the one hour feeding period stimulated an increase in *M*.
5. Change in body heat content over the feeding period

represented heat storage in the WARM treatment, but loss of heat from the body equal to 40, 33 and 26% of the total HW in the TURHAY, COLD and FROZEN treatments.

6. The balance predicted an increase in H over the cooling period in the WARM and TURHAY treatments. Although in the WARM treatment, mean skin temperature did rise above pre-cooling values after cooling, a slight drop occurred during feeding/cooling. Thus unless evaporative heat loss increased during feeding/cooling the model under-estimated heat flow from the body. The predicted H of the FROZEN treatment of 1.27 MJ per hour is similar to the fasting heat production of 1.24 MJ which was calculated for these steers from a mean literature value of 70 W.m^{-2} (Thompson, 1973).

6.5 Summary Experiments V, VI and VII

Rumen cooling appeared to be an acceptable alternative to the eating of cold feed in the study of the effects of HW within certain limits imposed by the relative volumes of the rumen and the food. This conclusion was based on the small percentage of the warming (<20%) which occurred before the rumen and from a direct comparison in which HW was provided either via the mouth or predominately through the rumen which showed little important difference between the two sites of cooling.

Any increase in metabolic rate which occurred in response to HW appeared to be only temporary over the latter stages of feeding and for the ensuing 1 to 2 hours. No evidence of a change in basal (15 h post-feeding) metabolic rate was detected.

The substitution of part of a high moisture feed by a high dry matter but lower digestibility feed did not influence the effect of HW in any obvious way other than would be expected from the decrease in HW due to the substitution.

A model using data obtained in these experiments showed heat flow into the rumen from the body in response to a reduction in rumen temperature by consuming cold feed could be large and equivalent to >60% of the pre-cooling heat loss to the environment. The increase in metabolic rate was insufficient to cover this heat flow into the rumen and a heat debt occurred in the body heat content. In this experiment the body heat debt was fully recovered six hours after the cooling took place.

7. EXPERIMENTS VIII and IX ENERGY BALANCE STUDIES AND THE HEAT OF WARMING

Results from the previous experiments indicated that effects of the heat of warming (HW) on animals were dependent not only on the level of HW (Experiment I and V) but also on the level of feed intake (Experiment III). It is possible that over a wide range of energy intake and HW that an interaction may exist between feed intake and HW.

Although no important carry-over influence of the effects of HW from one feeding period to another occurred when feeding periods were 6 h apart (Experiment V), the effects of HW were persistent for at least two hours after rumen cooling/feeding (Experiments I and III). More frequent feeding and cooling are likely to occur under natural grazing of high moisture feeds.

Extrapolation from short-term measurements (Experiment V, 4 h duration) conducted at one feed intake indicated that any increase in M due to HW was small on a daily basis. However, complete energy balance studies should permit better interpretation of such increases in M in terms of energy retention and possible changes induced by HW in the nutritive value of a feed.

Experiments VIII and IX were designed to examine longer-term (2 week) effects of various combinations of HW and feed intake.

7.1 Experiment VIII Energy balance of young sheep at five levels of energy intake and five levels of the heat of warming

Experiment VIII was designed to incorporate a wide range of HW and energy intake (IE) in an energy balance trial with frequently fed young sheep. The objective was to identify any important interactions between HW and feeding level which might require further analysis and to determine whether high levels of moisture and/or cooling had an effect on chemical or heat energy losses from the body.

This Experiment approached HW more from a nutritional (or daily energy balance) standpoint, rather than as a physiological study as had been the approach in earlier experiments.

Five levels of energy intake, each fed at five levels of ruminal cooling (HW) were incorporated into a Greco-Latin square involving five lambs.

7.1.1 Experimental Methods

7.1.1.1 Animals

Five Suffolk cross-bred, 6 month old wether lambs of a mean liveweight of 34.8 ± 1.0 kg and with a fleece depth of 5 to 6 cm were selected. Two weeks before the experiment began the lambs were fitted with an intra-ruminal infusion tube. These tubes were fitted into the sheep at the normal site for a rumen fistula (Hecker, 1974) under local anaesthesia (procaine hydrochloride, Novocain, Winthrob

Laboratory). Following a 2 cm cutaneous incision, the subcutaneous muscle layers were penetrated by blunt dissection and the rumen epithelium was drawn up to the skin and sutured in three places. A PVC catheter (Canlab Ltd., laboratory grade) was inserted into the rumen through a 13 gauge needle and secured with a purse-string suture. A small (3 mm) permanent fistula was established in four out of five cases by this technique. In the fifth lamb the resulting fistula was larger and leakage of rumen fluid occurred and a 1 cm rubber cannula was inserted. Small fistulae were considered preferable in this experiment to minimise the possibility of heat loss from the rumen.

The lambs were accustomed to the experimental schedule before the experiment began.

7.1.1.2 Feed Intake and Heat of Warming Treatments

During the five 21 day periods, each lamb experienced one combination of each level of energy intake and ruminal cooling as shown in Table 7.1.

7.1.1.3 Levels of energy intake and heat of warming

A concentrate barley alfalfa pellet (Ration A) was fed at five levels, 20, 35, 55, 80 and 110 g air dry feed.kg LW^{-0.75}.day⁻¹. Intake levels were calculated individually for each lamb from liveweight on day 1 of each period.

The daily ration was fed in 6 equal portions at 3 hourly intervals from 0830 h by a mechanical automated

Table 7.1 Greco-Latin square design (Experiment VIII)

		Period				
		I	II	III	IV	V
Lamb 14	IE ¹ HW	35 COLD	110 HOT	20 DRY	80 WARM	55 COOL
Lamb 20	IE HW	110 COOL	80 COLD	55 WARM	20 HOT	35 DRY
Lamb 38	IE HW	20 WARM	55 DRY	110 COLD	35 COOL	80 HOT
Lamb 41	IE HW	55 HOT	35 WARM	80 COOL	110 DRY	20 COLD
Lamb 42	IE HW	80 DRY	20 COOL	35 HOT	55 COLD	110 WARM

¹ IE = Levels of energy intake
20, 35, 55, 80, 110 g fresh feed.kg LW^{-0.75}.day⁻¹

HW = Heat of Warming treatments, water infused
at 2, 12, 22 or 38°C for COLD, COOL,
WARM and HOT or fed dry (DRY)

feeder which deposited each meal in the feed box over approximately seven minutes.

The ruminal cooling (HW) treatments were by rumen infusions of tap water. The quantity of water infused was equivalent to feeding a 10% dry matter ration. The temperature of the infusate was 38.0, 22.0, 12.0 or 2.0°C, designated HOT, WARM, COOL and COLD treatments respectively. For the fifth HW treatment the ration was fed with no

supplementary water infusion (DRY).

Infusions were made by a finger pump (Harvard Apparatus Co., Infusion-Withdrawal Pump, Model 955) over 6x1 h periods at 2 h intervals beginning at 0830 h. The various infusion rates were achieved by altering the rate of delivery of the pump and by the diameter of the delivery tubes (Technicon Autoanalyser tubing). The infusions were maintained at the desired temperature at entry to the rumen by insulated catheter covers (see Experiment I).

7.1.1.4 Measurements

Feed and water intake, faecal and urine output and liveweight

During each period, days 1 to 10 were allowed for adjustment from the previous intake and HW treatments. Daily faecal and urine collections were made from day 11 to 20. Fresh faecal weight was recorded and a sub-sample dried (48 h at 70°C) for subsequent dry matter and intake energy determinations. Urine was collected under acidic conditions (80 ml 3 M hydrochloric acid). Urine volume was recorded daily and an aliquot bulked over the 10 day collection period for subsequent energy and nitrogen analysis. Feed residue which only occurred on the 80 and 110 intakes was recorded daily as was the volume of any residual infusate. Drinking water intake, corrected for evaporation was recorded over five days from day 11. Energy content of feed, faeces and urine was measured by standard bomb

calorimetry (Parr Adiabatic Calorimeter, Model 1241) and nitrogen content of the urine was determined by the Kjeldahl procedure (AOAC, 1965).

On day 21 of each period all lambs were fed at the 55 intake level and received the COOL ruminal infusion treatment to reduce variation in gut fill before weighing the following day.

Respiratory Gaseous Exchange

Oxygen consumption was measured continuously for 23 h beginning at 0830 h on two occasions 2 days apart during days 16 to 20 inclusive of each period. System A was used for one of the measurements and System B for the other measurement on the same lamb, except in Period I when system A was used for all measurements. When system A was used, carbon dioxide and methane production was also measured. A malfunction of the methane analyser prevented measurement of methane production in Periods II and III. Air flow through the ventilated hoods was 30 to 60 litres.min⁻¹ STP, the lower rates being used with the lower feed intakes.

At the conclusion of the above treatments four of the lambs were fasted for four days and oxygen consumption was measured for two periods of 30 minutes one hour apart (Fasting Heat Production, FHP). The lambs were then shorn (1.23 ± 0.34 kg wool) and weighed.

Standing-Lying Behaviour

During early periods of the experiment subjective observation revealed that standing-lying behaviour might be

modified while the lambs were in the hood. Consequently standing and lying time was monitored continuously for 23 h over days 16 to 20 during the latter three periods of the Experiment. A light string round the trunk of each lamb was flexibly attached to a micro-switch mounted above the metabolic crate and an event recorder (Esterline Angus Co.) recorded the duration of lying and standing. The total standing time over 23 h on days prior to, during and after enclosure in the hood was calculated.

Body temperature measurements

Rectal, ear and trunk skin and rumen core temperature and the temperature of the rumen infusate were recorded simultaneously on all lambs for 23 h continuously from 1700 h on day 13. Where more than three consecutive 30 min temperature records were not available the daily mean temperature was calculated as a weighed mean. The weighting factor for each half hour period was calculated from all complete data for each body temperature.

Statistical analysis

The standing-lying data which was not complete for all treatment combinations was analysed by a least squares analyses of variance for unequal numbers. All other data were statistically analysed as a Latin square with feed intake, HW treatment, sheep and periods as the main fixed sources of variance giving 8 df for error.

7.1.2 Results and Discussion

7.1.2.1 Feed Intakes and Heat of Warming Achieved

The actual mean daily feed intakes achieved were 20.3, 35.2, 54.8, 74.8 and 98.4 g fresh feed.kg LW^{-0.75}.day⁻¹ for the designed 20, 35, 55, 80 and 110 feed intakes respectively. At the two higher feeding levels small feed refusals were occasionally recorded. Feed consumed was calculated on the basis of the *mean* liveweight during the period but feed offered in each period was based on the liveweight of each lamb at the *beginning* of each period. Thus at higher feeding levels where the lambs gained weight, feed consumed was slightly below the designed intake.

With the DRY treatment sheep drank 0.47 litres water per day at the 20 intake level and water intake rose to 3.56 litres at the 110 intake level. Drinking water contributed up to 85% of HW in the DRY treatment. The greatest contribution (24%) of food to HW was with the 38°C infusion treatment. In all other treatments the main source of HW was from the infused water.

The total daily HW per lamb per 24 h for each intake level and infusion temperature is shown in Table 7.2. HW per day ranged from 0.04 MJ at the 20-HOT treatment to 2.08 MJ for the 110-COLD treatment which is a 52 fold range. HW per unit of digestible energy (DE) intake was relatively constant across intake levels but increased 10 times from the HOT infusion treatment to the COLD infusion.

Table 7.2 Total heat of warming ($\text{MJ}\cdot\text{day}^{-1}$) for each combination of energy intake and infusion temperature (Experiment VIII)

Infusion temperature		Feed intake ($\text{g}\cdot\text{kg LW}^{-0.75}\cdot\text{day}^{-1}$)					HW/DE ¹
Design	Actual	20	35	55	80	110	
38.5	37.4 ± 1.4	0.04	0.05	0.07	0.13	0.12	9 ± 1.8
DRY	DRY	0.07	0.13	0.26	0.17	0.46	22 ± 3.0
22.0	21.8 ± 1.0	0.19	0.29	0.58	0.73	0.99	56 ± 2
12.0	11.5 ± 0.6	0.30	0.55	0.91	0.95	1.55	87 ± 3
2.0	2.5 ± 0.7	0.45	0.73	1.02	1.50	2.08	119 ± 3
HW/DE		56	58	59	56	65	SEM = ± 10

¹ HW = Heat of Warming ($\text{kJ}\cdot\text{day}^{-1}$)

DE = Digestible energy intake ($\text{MJ}\cdot\text{day}^{-1}$)

7.1.2.2 Digestibility of Dry Matter and Gross Energy

Digestible dry matter (DDM) and digestible energy coefficients for each intake and HW combination are shown in Table 7.3. There was a significant difference in both digestibility coefficients due to intake level. An orthogonal comparison indicated a high linear component in the feed intake treatment variance. The simple regression equation of digestible energy (DE) on intake energy (IE) was

$$Y = 0.770 - 0.056(\pm 0.009)X \dots\dots\dots(7)$$

$$R^2 = 0.60, \text{ RSE} = \pm 0.021 \text{ MJ DE}\cdot\text{MJ IE}^{-1}$$

where Y = digestible energy intake per unit of intake energy

Table 7.3 Digestible dry matter and digestible energy coefficients for five feed intakes and 5 levels of heat of warming (Experiment VIII)

HW treatment	Feed intake treatment					HW mean
	20	35	55	80	110	
Dry matter digestibility (g DDM.g DM ⁻¹)						
HOT	0.770	0.755	0.751	0.693	0.708	0.735
DRY	0.766	0.718	0.727	0.709	0.702	0.724
WARM	0.743	0.768	0.757	0.704	0.665	0.727
COOL	0.743	0.759	0.744	0.743	0.655	0.729
COLD	0.763	0.735	0.717	0.693	0.704	0.722
Feed intake mean	0.757a	0.747ab	0.739ab	0.708bc	0.687c	±SEM 0.007
Digestible energy (kJ DE.kJ GE ⁻¹)						
HOT	0.752	0.747	0.750	0.706	0.696	0.730
DRY	0.767	0.707	0.716	0.702	0.689	0.716
WARM	0.737	0.755	0.753	0.692	0.649	0.717
COOL	0.727	0.753	0.737	0.736	0.650	0.721
COLD	0.751	0.728	0.704	0.675	0.696	0.711
Feed intake mean	0.746a	0.738ab	0.732ab	0.702bc	0.676c	±SEM 0.006

Each value is one digestibility trial with one lamb

a,b,c,d means in rows followed by the same letter are not significantly different (p<0.05)

(MJ DE.MJ IE⁻¹ and X = intake energy per unit metabolic weight (MJ IE.kg LW^{-0.75}.day⁻¹) This relationship predicted a decrease in the digestibility of gross energy of 0.038 for an increase in feed intake from 40 to 80 g.kg LW^{-0.75}.day⁻¹, i.e. from maintenance to twice maintenance. Similar declines in digestibility with increasing feed intake have been recorded many times (Blaxter, 1962; Schneider and Flatt, 1975).

There was no statistical evidence that digestibility of dry matter or intake energy was influenced by HW treatments. The regression coefficient for HW in the multiple regression equation of digestibility on IE and HW was negative but small and not statistically significant. Over the range of HW per unit IE of 8 to 88 kJ.MJ⁻¹, DE coefficient was predicted to fall from 0.775 to 0.763 or 1.5% which is of little practical importance. Other reports have failed to show a significant effect of snow as a source of water (Sims and Butcher, 1973) or rumen loading with cold water (Cunningham et al., 1964; Battachyra and Warner, 1968; Brod, 1979) on digestibility.

7.1.2.3 Standing Time

The total time per 23 h that the lambs stood while in the ventilated hood was reduced significantly ($p < 0.05$) compared to the time spent standing on days prior to, or after the respiratory gaseous exchange measurements (Figure 7.1). The reduction was 100 min or 23% of normal standing

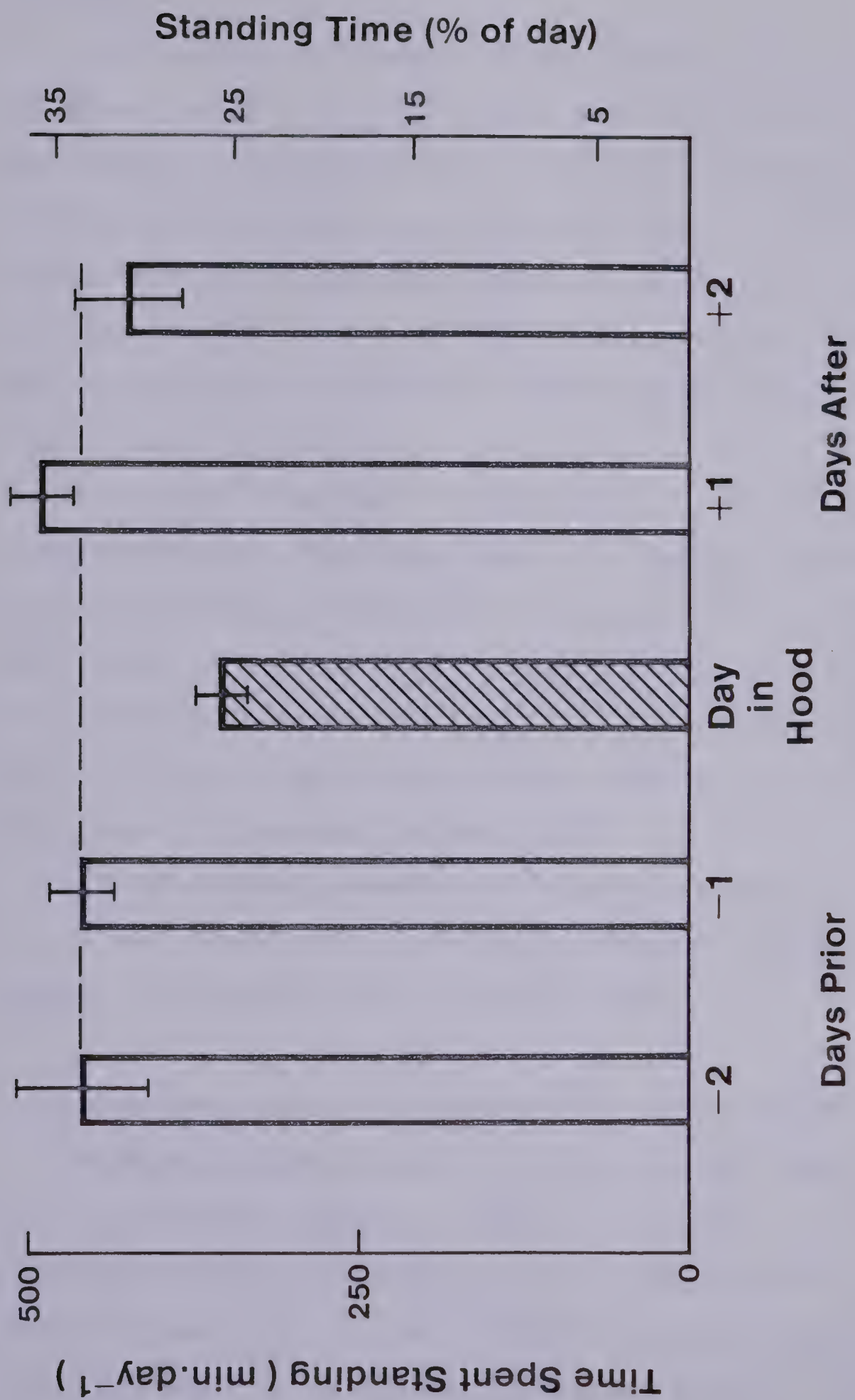


Figure 7.1 Daily standing time of lambs before, during and after enclosure in a ventilated hood (Experiment VIII)

time. There was no significant effect of feeding level or HW treatment.

The freedom of movement of the lambs in the hood did not appear to be restricted since the lambs stood up and lay down freely. The background noise level in the experimental room was 72dB but was only 62dB in the hood. When the level in the room was raised 23dB, there was 15dB less noise in the hood than in the room. The reduced standing time may have been a result of less disturbance by extraneous noise in the hood.

In another experiment (Nicol et al., 1979) which ran concurrently with this experiment, the energy expenditure of similar sheep when standing was $19 \text{ J.kg}^{-1}.\text{min}^{-1}$ higher than when lying. This additional energy expenditure associated with standing is within the range of other estimates (Osuji, 1974) and similar to a more recently published value of $22 \text{ J.kg}^{-1}.\text{min}^{-1}$ (Davey and Holmes, 1977)

All daily heat production measurements were raised by 0.08 MJ per lamb ($19.0 \text{ J} \times 42 \text{ kg liveweight} \times 100 \text{ min}$) to account for the additional standing time.

7.1.2.4 Methane Production and Metabolisable Energy Intake

Methane production over a 23 h period was recorded from only 14 of the 25 gaseous exchange measurements, but a further 9 observations were available from Experiment IX using the same ration, feed intake levels and sheep as in this experiment. The combined data were used to calculate

the methane energy losses as a percentage of IE. The resultant linear regression equation was:-

$$Y = 148 - 3.8(\pm 0.5)X \dots\dots\dots(8)$$

$$R^2 = 0.83, RSE = \pm 15 \text{ kJ methane.MJ IE}^{-1}$$

where Y = Methane energy (kJ methane.MJ IE⁻¹.day⁻¹) and X = IE intake (MJ).

This equation predicted methane energy losses of 11% at a IE intake of approximately maintenance and a fall to 8% at 2x maintenance. These levels are slightly higher than Blaxter (1962) reported for a range of pelleted feeds.

Equation 8 was used to predict methane losses for each IE intake in this trial. Since the methane data were not complete for all of the treatment combinations and because no obvious trend in methane production with HW treatment existed, no attempt was made to adjust methane losses for HW treatment.

Urine energy losses varied from 7.7% of IE on the 20 intake to 3.7% of IE at the 110 intake level. This decrease in urine energy losses as a percentage of IE represented a reduction of 0.7 percentage units for a doubling of feed intake. A decline of between 0.6 and 0.8 percentage units in urine energy as feed intake doubles was consistent with previous reports (ARC, 1965).

Metabolisable energy intake was calculated for each intake and HW treatment combination from the actual IE intake, faecal, and urine energy losses for each lamb and predicted methane losses. The IE concentration of the

pelleted barley alfalfa ration (Ration A) was 18.1 ± 0.1 MJ.kg⁻¹ dry matter. Metabolisable energy (ME) intakes are shown in Table 7.4.

Metabolisable energy intake increased significantly with increasing feed intake but was not significantly influenced by HW treatments. The metabolisability of IE (ME/IE) was not influenced significantly by either treatment. The mean metabolisability was 0.570 MJ ME.MJ⁻¹ IE, equivalent to a ME concentration in the dry matter of 10.3 MJ.kg⁻¹ feed dry matter.

The metabolisability of DE increased with feed intake by 2.4 percentage units as feed intake doubled. ME/DE at maintenance was 0.800. Although earlier work suggested that ME/DE declines slightly as intake increases (ARC, 1965), more recent analysis of many studies (Blaxter and Boyne, 1978) showed that a decrease does not always occur and a small increase may occur if the relative decline in DE with increasing intake is greater than the decline in urine and methane losses.

7.1.2.5 Daily Heat Production

Heat production measured by system A and B was compared. For 22 paired measurements (one lamb on both systems 1 to 2 days apart) the regression of system 1 on system 2 was

$$Y = 0.10 + 0.98(\pm 0.06)X \dots\dots\dots(9)$$

$$R^2 = 0.93, RSE = \pm 0.53 \text{ MJ}$$

Table 7.4 Daily metabolisable energy intake, heat production and energy retention for individual lambs (Experiment VIII)

HW Treatment	Feed intake treatment					HW Mean
	20	35	55	80	110	
Metabolisable energy intake (MJ.day ⁻¹)						
HOT	2.73	4.35	6.94	10.66	14.04	7.74
DRY	2.98	4.75	6.34	10.32	14.31	7.74
WARM	2.66	4.10	8.50	11.08	12.75	7.82
COOL	2.38	4.77	8.68	10.32	13.69	7.97
COLD	2.86	4.70	6.61	9.16	13.86	7.44
Feed intake mean	2.72a	4.53a	7.41b	10.31c	13.73d	±SEM 0.31
Heat production (MJ.day ⁻¹)						
HOT	3.60	4.27	5.18	7.85	9.13	6.01
DRY	3.74	4.96	5.08	7.98	9.16	6.18
WARM	3.78	3.88	6.13	7.43	8.90	6.02
COOL	3.97	4.82	6.22	7.20	8.68	6.18
COLD	4.28	5.07	5.81	7.04	8.65	6.17
Feed intake mean	3.87a	4.60ab	5.68b	7.50c	8.90c	±SEM 0.26
Energy retention (MJ.day ⁻¹)						
HOT	-0.87	0.08	1.76	2.81	4.91	1.74
DRY	-0.87	-0.21	1.26	2.34	5.15	1.53
WARM	-1.12	0.22	2.37	3.64	3.85	1.79
COOL	-1.59	-0.05	2.46	3.12	5.01	1.79
COLD	-1.42	-0.37	0.80	2.12	5.21	1.27
Feed intake mean	-1.17a	-0.07a	1.73b	2.81b	4.82c	±SEM 0.17

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

where Y = heat production (MJ) by system B and X = heat production measured by system A. There was little systematic difference between the systems and no correction was made for the respiratory gas analysis system used.

Heat production measured on the first and second occasion were also compared by regression analysis with the following result.

$$Y = 0.26 + 1.05(\pm 0.06)X \dots\dots\dots(10)$$

$$R^2 = 0.93, RSE = \pm 0.53 \text{ MJ}$$

where Y = heat production ($\text{MJ}\cdot\text{day}^{-1}$) measured on day 2 and X = heat production measured on the first occasion. There was little difference between successive measurements giving confidence that the lambs were well adjusted to the indirect calorimetric techniques used.

The mean heat production (M) for each feed intake and HW combination is shown in Table 7.4. There was no significant difference in heat production due to HW treatments but the feed intake effect was statistically significant ($p < 0.05$).

7.1.2.6 Fasting Heat Production

Fasting heat production, measured at the end of the experiment was variable between the first and second 30 min measurement. The lambs appeared to be more excited than during the main calorimetry runs. The lower of the two measurements on each sheep was used as the estimate of fasting heat production. The mean value was $232 \text{ kJ}\cdot\text{kg}$

$\text{LW}^{-0.75} \cdot \text{day}^{-1}$ on the basis of unfasted, woolly liveweight or $254 \text{ kJ} \cdot \text{kg} \text{ LW}^{-0.75} \cdot \text{day}^{-1}$ fasted, fleece-free liveweight. This latter value is similar to other published values for the fasting heat production of sheep which range from 239 to 269 $\text{kJ} \cdot \text{kg} \text{ LW}^{-0.75} \cdot \text{day}^{-1}$ (Blaxter, 1962; Graham, 1967; Rattray et al., 1973) and suggested that these woolly sheep, in the absence of any HW were in thermoneutrality.

7.1.2.7 Energy Retention

Heat production was subtracted from ME intake for each treatment combination to give energy retention (RE, $\text{MJ} \cdot \text{day}^{-1}$) shown in Table 7.4. Energy retention increased significantly ($p < 0.05$) as ME intake increased but was unaffected by HW treatment. The relationship between RE and ME intake per unit metabolic weight is shown in Figure 7.2. Conventional linear regressions of RE on ME intake above and below zero energy retention revealed an efficiency of utilisation of ME for maintenance (km) of 73.5% and efficiency for production (kpf) of 50.8%. For a ME/IE of 57.0% measured in this Experiment the ARC (1965) equations would predict a km and kpf of 71.7 and 49.2 respectively. The positive energy balance equation predicted the requirement of ME for maintenance to be $293 \text{ kJ} \cdot \text{kg} \text{ LW}^{-0.75} \cdot \text{day}^{-1}$ and the equation below zero energy balance gave a figure of $306 \text{ kJ} \cdot \text{kg} \text{ LW}^{-0.75} \cdot \text{day}^{-1}$.

The Greco-Latin square design used in this Experiment does not permit the statistical analysis of interactions

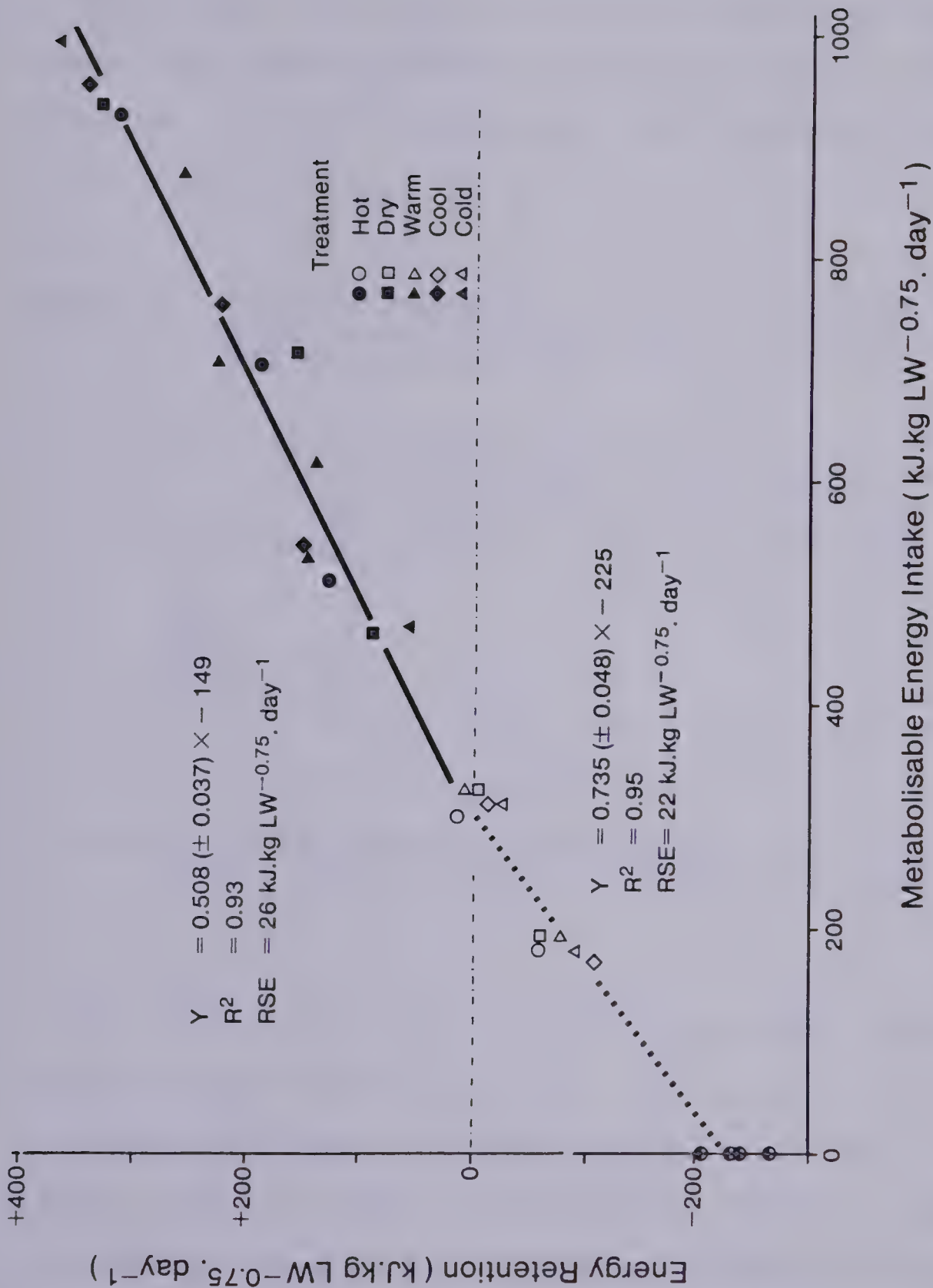


Figure 7.2 Energy retention and metabolisable energy intake of lambs at five levels of feed intake (Experiment VII), solid lines and symbols positive energy balance; broken line and open symbols, negative energy balance) Each symbol represents one balance trial

between the main treatment effects. However, energy retention data showed a trend towards a decline in RE with increasing HW at low ME intake but not at the higher levels of feed intake. A division has been drawn within each intake level between consecutive HW levels which show a >50% reduction in RE over the mean of lower HW levels (Table 7.5).

Table 7.5 Feed intake by heat of warming treatments which reduce energy retention by more than 50% (Experiment VIII)

	Feed intake treatment				
	20	35	55	80	110
HOT	-	-	-	-	-
DRY	-	-	-	-	-
WARM	xxx	-	-	-	-
COOL	xxx	xxx	-	-	-
COLD	xxx	xxx	xxx	xxx	-

xxx Energy retention reduced 50% below mean of lower cooling levels within each level of intake

By this arbitrary division, RE in the treatment combinations xxx were reduced by 50%.

Above maintenance ($>40 \text{ g feed.kg LW}^{-0.75}.\text{day}^{-1}$) HW greater than 8% of DE (COLD treatment) reduced energy retention by 50%, but at low levels of feeding HW equivalent to the consumption of the ration at 22°C (WARM treatment) was sufficient to reduce energy retention by 50%.

Although neither ME intake nor M was significantly affected by HW treatment, any effect of HW treatment on RE is likely to be by an increase in M rather than a decrease in ME intake. An illustration of a possible interaction between M and HW is shown in Figure 7.3. M and M-HW (M less total daily HW) have been plotted for the 20 and 110 feed intake levels. At the low level of feed intake M rises by almost 20% from the lowest to highest HW, while M at the highest feed intake remains relatively constant with increasing levels of HW.

When HW is deducted from M, a relatively constant level of M is indicated at the low level of feed intake and a large drop is shown for the high feed intake. This model suggests that at low energy intake where M is not greatly above minimum heat loss, then M is elevated to meet HW. Fasting heat production measured in this Experiment would suggest minimum heat loss was 3.50 MJ per lamb per day. On the other hand at high energy intake, M is sufficiently high that M-HW is above minimum heat loss at all levels of HW and no increase in M is required to cover HW. This conclusion is consistent with earlier work in this study (Experiment III) which showed a much reduced response to ruminal cooling where feed intake was increased.

By reference to Tables 7.2 and 7.5, the same total quantity of HW, for example $0.73 \text{ MJ}\cdot\text{day}^{-1}$, at the 80 feed intake had apparently little effect on M whereas at low (35) intake levels M may have increased with the same daily HW.

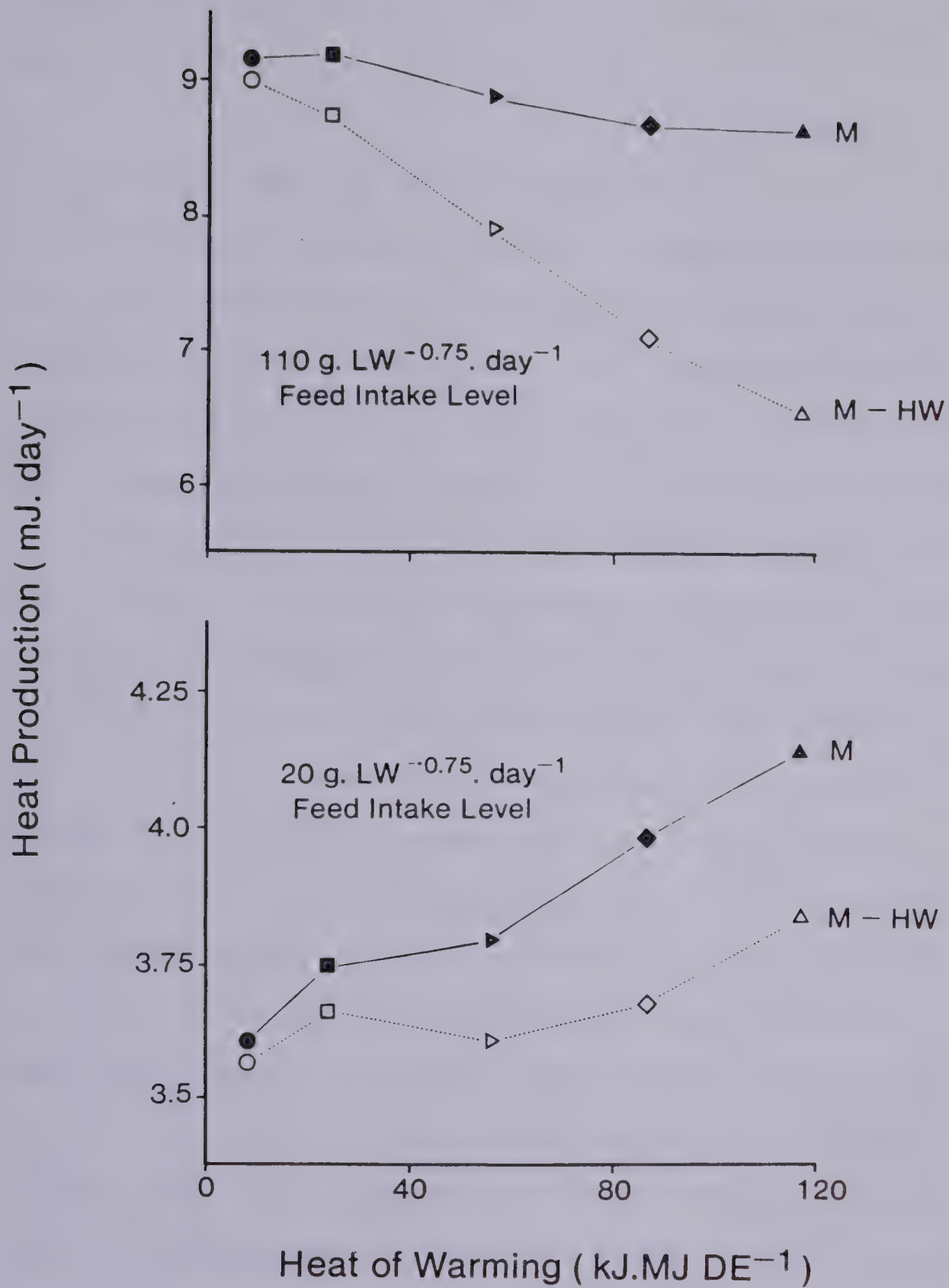


Figure 7.3 Heat production (solid line) and heat production less the heat of warming (broken line) of lambs fed two levels of feed intake and receiving five levels of the heat of warming (Experiment VIII)

The level of feed intake appears to be much more important to the ultimate effects of HW on M than the level of HW per se.

7.1.2.8 Rumen and Ear skin Temperature

Daily mean rumen and ear skin temperatures were the only body temperatures recorded which showed significant treatment effects (Table 7.6). The effects of both the feed intake level and ruminal cooling treatment on rumen and ear skin temperature were in accord with previous experiments.

Although mean daily ear skin temperature declined with feed intake, no significant effect of ruminal cooling treatment was observed. However the individual standard errors of the ruminal cooling treatment means show that the daily variation in ear skin temperature was greater with increasing levels of ruminal cooling. This greater variation in ear skin temperature was a reflection of a fall in ear skin temperature with cooling and recovery after cooling. While ear skin temperature declined with increasing ruminal cooling at the high levels of feed intake, the effect was not as marked at the low feed intakes. Ear skin temperature in fact showed a slight rise with increasing ruminal cooling at the lowest feed intake level.

Mean daily rumen temperature was reduced by up to 1°C with the higher levels of ruminal cooling but this reduction did not decrease the apparent digestibility of the ration.

Table 7.6 Mean daily ear skin and rumen temperature for all feed intake and heat of warming treatment combinations (Experiment VIII)

HW treatment	Feed intake level					HW mean
	20	35	55	80	110	
Ear skin temperature (°C)						
HOT	12.4	16.6	27.2	29.3	34.2	23.9±0.71 ¹
DRY	16.0	13.0	17.8	27.4	33.5	21.5±0.98
WARM	15.4	13.6	26.9	18.2	23.7	19.6±1.09
COOL	16.3	16.8	13.7	29.8	21.3	19.6±1.14
COLD	21.0	12.3	9.8	23.4	23.3	18.0±1.27
Feed intake mean	16.2a	14.5a	19.1ab	25.6b	27.2b	±SEM 2.1
Rumen core temperature (°C)						
HOT	38.8	38.7	39.1	39.0	38.7	38.9e
DRY	39.0	39.3	39.0	39.4	39.4	39.2e
WARM	38.5	38.4	38.7	38.7	38.4	38.5f
COOL	38.4	37.9	38.3	38.2	38.5	38.3f
COLD	37.9	38.1	37.1	38.2	37.8	37.8g
Feed intake mean	38.5	38.5	38.4	38.7	38.6	±SEM 0.12

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

¹ Standard errors for individual HW treatments

Rumen temperature did not rise with increasing feed intake. Although HW of each ruminal cooling treatment relative to energy intake was constant as energy intake level increased (see Table 7.2), the *rate* of cooling increased as feeding level increased. A more rapid cooling rate induced a greater decrease in rumen temperature (Experiment II). The more rapid cooling rates at the higher feed intakes may have negated the increase in rumen temperature which might have been anticipated at the higher feeding levels.

7.2 Experiment IX The influence of feeding level and heat of warming on the heat production of sheep

Experiment IX was designed to further examine the possible interaction between the effect of HW and energy intake on heat production which appeared to exist in Experiment VIII. Such an interaction would have potentially important practical implications in determining feeding levels of high moisture feeds.

7.2.1 Experimental design

The heat production of four young sheep at five levels of feed intake with two levels of ruminal cooling was compared.

7.2.1.1 Feed intake and Rumen Cooling Treatments

The five feeding levels were those used in Experiment VIII, namely 20, 35, 55, 80 and 110 g feed.kg LW^{-0.75}.day⁻¹. The automatic feeding system and timing of feeding were those used in Experiment VIII. The two ruminal cooling treatments were the extremes of the five levels used in the previous experiment; the HOT treatment, a ruminal infusion of water at 38.0°C and the COLD treatment, water infused at 2.0°C. The quantity of water infused was determined by the feeding level and was such that the effective dry matter percentage of the feed was 10%.

7.2.1.2 Animals

Four of the sheep used in Experiment VIII were used in this experiment. The mean liveweight was 47.0 ± 1.8 kg and they were approximately 10 months old. Fleece depth was 3.8 ± 0.2 cm at the beginning of the 10 week experiment and increased to 7.1 ± 1.1 cm by the end of the 10th week when the sheep were shorn (1.4 ± 0.1 kg wool). Ruminal infusion catheters were installed as in Experiment VIII.

7.2.1.3 Design

The experiment consisted of 10 seven day periods. Two of the sheep (14 and 38) began the experiment at the 20 feed intake level and increased to the next highest feed intake level at weekly intervals. Sheep 14 received the HOT ruminal infusion treatment and sheep 38 the COLD treatment for the first five weeks. After five weeks, by which time the sheep had experienced all five feed intake levels at one ruminal infusion temperature, the ruminal infusion treatments were reversed and feed intake declined weekly through the five levels. The remaining two sheep followed the reverse design. These two sheep (20 and 41) began at the highest feed intake, proceeded weekly to the lowest, changed ruminal infusion treatment and increased through all feeding levels over the final five weeks of the experiment. Feed intake was based on the mean liveweight of each sheep pair before feeding on day 1 of each period. One sheep (41) died of undeterminable causes during Period 9 when on the

80-COLD treatment. A substitute sheep (32) was available and used in Period 10 but the data were incomplete for Period 9.

7.2.1.4 Measurements

Total faecal collections were made from day 2 to 7 of each period throughout the experiment and sub-samples dried daily.

Respiratory gaseous exchange measurements were made over continuous periods of 7 h on all sheep on day 6 of each period. The gaseous exchange of two sheep (14 and 38) was always made from 0900 to 1600 h and the other two sheep (20 and 41 or 32) from 1700 to 2400 h.

On the basis of the 24 h heat production measurements made in Experiment VIII, these 7 h periods were equal to 29.7 and 30.1% of total daily production for the am and pm measurements respectively.

Respiratory gas analysis system A was used on sheep 14 and 41 or 32 and system B on the other two sheep (20 and 38).

7.2.1.5 Statistical analysis

Heat production data were analysed by least squares analysis of variance for unequal numbers with feed intake level, ruminal infusion treatment and previous feeding level (feed intake in the previous period) as the main effects.

7.2.2 Results and Discussion

Daily heat production rose significantly ($p < 0.05$) with feed intake (Table 7.7). Previous feeding level also significantly influenced heat production. When measured during a rising sequence of feed intake levels, i.e. when previous feeding level was low, heat production was 5% below the mean M for the feeding level measured. Conversely, when heat production was measured on a declining feed intake sequence, M was 5% above the mean. Total faecal output over days 2 to 7 of each period showed a similar carry over effect of $\pm 6\%$. The carry over effects were consistent across intake levels.

Heat production was not significantly influenced by rumen cooling treatment nor did the interaction of ruminal cooling treatment with intake level reach statistical significance. However, the same trend existed as in Experiment VIII towards higher heat production with the higher levels of ruminal cooling at low feed intakes but not at higher intakes. The apparent increase in M at the 20 feed intake was equal to 81% of the difference in HW between the COLD and WARM ruminal infusion treatments. At the 80 intake level the difference in M between the COLD and HOT treatments was equivalent to only 3% of the ruminal cooling.

Taking the ME concentration of the ration to be 10.3 MJ.kg⁻¹ dry matter (measured in Experiment VIII), ME intake and energy retention (RE) were calculated for each treatment combination and are shown in Table 7.7 together with energy

Table 7.7 Heat production, metabolisable energy intake and energy retention for the two ruminal cooling treatments (Experiments IX) and energy retention (Experiment VIII)

Ruminal infusion treatment	Feed intake treatment				
	20	35	55	80	110
(1) Experiment IX					
Heat production (MJ.day ⁻¹)					
HOT	4.33	5.29	6.54	8.38	10.66
COLD	4.86	5.66	6.70	8.42	10.43
Mean	4.60 ^a	5.47 ^{ab}	6.62 ^b	8.41 ^c	10.54 ^d
COLD-HOT	0.53	0.37	0.16	0.04	-0.23
% difference COLD-HOT	12.2	7.0	2.6	0.5	-2.0
Metabolisable energy intake (kJ.kg LW ^{-0.75} .day ⁻¹)					
HOT	205	305	488	720	912
COLD	208	311	485	704	903
COLD-HOT	3	6	-3	-16	-9
% difference COLD-HOT	1.5	2.0	-1.0	-2.2	-1.0
Energy retention (kJ.kg LW ^{-0.75} .day ⁻¹)					
HOT	-46	2	125	259	342
COLD	-78	-19	120	252	358
COLD-HOT	-32	-21	-5	-7	+16
(2) Experiment VIII					
Energy retention (kJ.kg LW ^{-0.75} .day ⁻¹)					
HOT	-55	+5	130	185	320
COLD	-90	-36	57	214	348
COLD-HOT	-35	-41	-73	+29	+28

^{a,b,c,d} means in rows followed by the same letter are not significantly different ($p < 0.05$)

retention data from Experiment VIII for comparison. The mean difference in ME intake between the COLD and HOT treatments was small (<2%) while large differences in RE occurred at the lower feed intakes.

In a conventional approach to calculating the efficiency of utilisation of ME for maintenance and gain in the COLD and HOT treatments, linear regressions of RE ($\text{kJ.kg LW}^{-0.75}.\text{day}^{-1}$) on ME intake ($\text{kJ.kg LW}^{-0.75}.\text{day}^{-1}$) were computed for below zero energy balance (FHP, the 20 and 35 feed intake levels) and positive energy balance (55,80 and 110 feed intake levels), (Table 7.8).

Table 7.8 Linear regressions of energy retention on metabolisable energy intake above and below zero energy retention (Experiment IX)

Infusion treatment	Regression coefficient b	Intercept a	R ²	RSE ¹
Negative energy balance				
HOT	0.780 ±0.057	-223	0.94	27
COLD	0.648 ±0.073	-225	0.87	35
Positive Energy Balance				
HOT	0.528 ±0.065	-195	0.87	45
COLD	0.612 ±0.060	-133	0.86	42

¹ Residual standard error ($\text{kJ.kg LW}^{-0.75}.\text{day}^{-1}$)

The efficiency of utilisation of ME for maintenance (km) with the WARM treatment was 13 percentage units higher than with the COLD treatment. The utilisation of ME above zero RE, (kpf) was 9 percentage units higher for the COLD treatment. The km and kpf equations predicted an increase in the ME for maintenance (zero energy retention) of 61 and 67 kJ.kg LW^{-0.75}.day⁻¹ respectively for the COLD treatment. This 24% increase in maintenance requirement was equivalent to an increase of 1.8 kJ.kg LW^{-0.75}.day⁻¹.°C⁻¹ difference in temperature between the ruminal infusion treatments.

The conventional apportioning of ME above and below zero RE has some biological basis (Blaxter, 1962) and is convenient for calculating feed requirements although a continuously variable efficiency may be preferable from a statistical standpoint (Blaxter and Boyne, 1978).

On the other hand there is no logical reason for the change in the relative effect of HW on km and kpf to be associated with zero energy balance. The changing effect of HW on efficiency of ME utilisation was a reflection of the progressive increase in HW as ME intake increases and the decreasing influence of HW on M as ME intake increases (Table 7.5).

7.3 Summary Experiments VIII and IX

A wide range of ruminal cooling treatments were found to have no major effects on faecal or urinary energy losses over a wide range of energy intakes.

There was a strong trend towards a reduction in energy retention with high levels of ruminal cooling at low feed intakes due to an apparent increase in heat production. The trend was absent at high feed intakes. These experiments demonstrated that a considerable (24%) increase in the ME requirement at maintenance may be caused by the consumption of a high moisture feed at 2°C in a 10°C ambient temperature.

The interaction of HW with feed intake level reduced the efficiency of utilisation of ME for maintenance, but increased the apparent utilisation of ME for energy gain. Energetically there would appear to be an advantage in feeding cold high moisture feeds at levels well above maintenance.

8. EXPERIMENTS X AND XI HEAT OF WARMING AND ACUTE CHANGES IN AMBIENT TEMPERATURE

Ambient temperature to this point has not been included as a variable in these experiments. Priority has been given to establishing relationships between the response of an animal to changes in the heat of warming independent of the effects of ambient temperature.

However, there is evidence that ambient temperature (T_a) does influence the response of an animal to HW (Holmes, 1970; 1971a). Under field conditions with high moisture feeds, there is an intimate relationship between T_a and HW. As T_a declines, HW would be expected to increase if feed intake remains constant. Therefore in Experiments X and XI the interaction of T_a with HW was examined by measuring the heat production at ambient temperatures from $+10^\circ$ to -20°C of cattle and sheep experiencing various levels of the heat of warming.

8.1 Experiment X

The heat production of steers at three ambient temperature following four levels of heat of warming

The oxygen consumption of steers fed turnips or turnips plus hay incorporating four levels of heat of warming was measured at ambient temperatures of $+10$, -8 and -20°C .

8.1.1 Experimental Methods

8.1.1.1 Animals

The animals used were those described in Experiment V; four 2.5 year old rumen fistulated steers weighing 406 ± 14 kg. All four steers were used for measurements at 10°C but only two (Horny and Polly) at -8 and -20°C .

8.1.1.2 Feeding and Heat of Warming Treatments

The experimental treatments were as in Experiment V, being 15 kg of WARM (27°C), COLD (2°C), FROZEN (-8°C) turnips or 10 kg of 2°C turnips plus 1 kg hay (TURHAY). All rations were fed twice daily. The HW per meal was 0.54, 1.54 1.96 and 5.27 MJ per steer during the 1 h eating period which was equivalent to a cooling rate during eating of 30, 87, 105 and 295 W.m^{-2} for the WARM, TURHAY, COLD and FROZEN treatments respectively.

8.1.1.3 Measurements

Oxygen consumption was continuously measured for two hours following the morning feeding period. The measurements at $+10^\circ\text{C}$ were made in conjunction with Experiment V on days 10 to 13 of each 14 day period. On day 14 of the period, the steers were moved immediately after the morning feeding period to a cold chamber pre-conditioned to $-20 \pm 3^\circ\text{C}$ with an air movement in the chamber at animal height of approximately 1 m.sec^{-1} .

At the end of Experiment V, the cold chamber was reset

to -8°C . The steers were held at $+10^{\circ}\text{C}$ and fed each of the four feed/HW treatments in random order on four successive mornings followed by the 2 h exposure at 8°C over which oxygen consumption was measured.

The steers did not appear to be disturbed by the change of location. The same ventilated hoods were used for all measurements. With the head of the steer in the ventilated hood, T_a in the hood was 1 to 2°C above the room temperature.

8.1.2 Results and Discussion

Mean heat production of the steers over the 2 h exposure at each ambient temperature was expressed per unit surface area and is shown in Table 8.1. Surface area (m^2) was taken as $0.09 \text{ LW}^{-0.66}$ (the Meeh formula, Blaxter, 1962).

Heat production increased with declining T_a with M at -20°C 52.7% greater ($p < 0.01$) than at $+10^{\circ}\text{C}$. As in Experiment V, M was higher in the post-feeding periods when FROZEN turnips had been fed.

Although there was no statistically significant difference in M between the first and second hour of measurement, the mean for the second hour was 8% below the first hour. This trend of a decrease in M during the second hour of exposure may have been a reflection of the decreasing impact of HW in the second hour after cooling and was greater with the higher levels of HW. There was no significant interaction between T_a and HW on M . The

Table 8.1 Heat production (W.m^{-2}) of steers over 2 h exposure to ambient temperatures of 10 and -20°C (Experiment X)

Feeding treatment	Ambient temperature ($^{\circ}\text{C}$)			Feeding treatment mean
	+10	-8	-20	
WARM	99	120	146	122 ^e
TURHAY	103	106	151	120 ^e
COLD	112	122	178	137 ^{ef}
FROZEN	127	149	195	157 ^f
<i>Ta</i> Mean	110 ^a	124 ^{ab}	168 ^b	

$$\text{SEM}(Ta) = \pm 9^{\circ}\text{C}, \quad \text{SEM}(\text{Feeds}) = \pm 11 \text{ W.m}^{-2}$$

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

difference in M between WARM and FROZEN treatments was relatively consistent, being 36, 58 and 49 W.m^{-2} at +10, -8 and -20°C respectively. On the basis of the statistical differences between treatments shown in Table 8.1, it was assumed that M had been increased by:-

1. Ta in all measurements at -20°C
2. HW in all measurements with FROZEN turnips and
3. the -8°C , COLD turnip treatment.

A linear multiple regression of M on Ta and HW (W.m^{-2}) was computed using the above data.

$$Y = 96 - 2.45(\pm 0.57)X_1 + 0.165(\pm 0.055)X_2, \dots (11)$$

$$R^2 = 0.83, \quad \text{RSE} = 13 \text{ W.m}^{-2}$$

where Y = heat production (W.m^{-2}), X_1 = ambient temperature

(°C) and X_2 = the heat of warming per meal expressed per body surface area (W.m^{-2}) Both regression coefficients were significant (X_1 , $p < 0.01$ and X_2 , $p < 0.05$). The simple correlation of M with T_a and HW were low ($R^2 = 0.43$ and 0.25 respectively) and not significant.

For a decline of 1°C in T_a , M increased by 2.45 W.m^{-2} . This figure is close to the value for total body conductance of steers of 2.4 W.m^{-2} given by Blaxter and Wainman (1961).

During the two hours of measurement, a change of 1°C in ambient temperature increased M to the same extent as 14 W.m^{-2} of HW in the previous hour.

The effect of HW on critical temperature (T_c) can be estimated using the formula from Blaxter (1962)

$$T_c = T_r - (M^* - E_{min} - G) \div C_t \dots\dots\dots(12)$$

where T_r = rectal temperature ($^\circ\text{C}$), M^* = thermoneutral heat production (108 W.m^{-2} in this Experiment), E_{min} = minimal evaporative heat loss (17 W.m^{-2} , Blaxter and Wainman, 1961) and G = heat of warming ($0.165 \times HW \text{ W.m}^{-2}$) C_t is the total body conductance of 2.45 W.m^{-2} .

With zero HW , critical temperature (T_c) was calculated to be -2.0°C . T_c increased to $+1.5$, $+5.4$, $+6.7$ and $+20.1^\circ\text{C}$ for the WARM, TURHAY, COLD and FROZEN treatments respectively. Further interpretation of these results is made in Section 9 of this study.

8.2 Experiment XI Heat production at two ambient temperatures of sheep at five feed intakes

The oxygen consumption of four sheep fed at five levels of feed intake each at two levels of HW was measured at ambient temperatures of +10 and -20°C.

8.2.1 Experimental Methods

8.2.1.1 Animals

The sheep used were those described in Experiment IX, i.e. 10 month old sheep, weighing 47 ± 1.5 kg and carrying 3 to 7 cm of fleece.

8.2.1.2 Feeding and rumen cooling (HW) treatments

The levels of feed intake and ruminal cooling (HW treatments) were described in detail in Experiment IX. The feeding levels were 20, 35, 55, 80 and 110 g.kg LW^{-0.75}.day⁻¹ of a pelleted concentrate ration (RATION A) and ruminal cooling was by water infused into the rumen at 38 and 2°C (HOT and COLD treatments).

8.2.1.3 Measurements

Oxygen consumption was measured at a Ta of +10 and -20°C on day 6 and 7 respectively of each seven day experimental period described in Experiment IX. For the -20°C measurement, the sheep were moved in pairs to the pre-conditioned cold chamber for a 7 h period over which the

appropriate feeding and cooling routine (Experiment IX) was maintained. Oxygen consumption was measured over the final four hours of the exposure and compared to oxygen consumption over the same time period at +10°C. One pair of sheep (14 and 38), at the same feed intake but one on the COLD and the other on the HOT ruminal infusion treatment, were measured from 1200 to 1600 h over a sequence (hours) of fed, not fed, not fed, fed. The second pair of sheep were exposed from 2000 to 2400 h and oxygen consumption measured over a sequence of not fed, fed, not fed, not fed. The combination of the two sequences gave the maximum feeding/rumen cooling periods (within the experimental design) in a four hour period.

8.2.2 Results and Discussion

Heat production calculated from the gaseous exchange measurements is shown in Table 8.2. In addition to a significant ($p < 0.01$) increase in heat production with feed intake which confirmed the results of Experiment IX, the analysis showed a significantly ($p < 0.05$) higher heat production with the COLD ruminal infusion. The increase in M with the decline in T_a was twice as great in the COLD than HOT treatment (Table 8.3).

The increase in M with decreased T_a in the COLD treatment was most marked at the higher levels of feed intake. At the low feed intake ($20 \text{ g.kg LW}^{-0.75} \cdot \text{day}^{-1}$), the increase in M (12%) due to the high level of rumen cooling

Table 8.2 Heat production of sheep (W.m^{-2}) during exposure to +10 and -20°C when fed at five levels of feed intake and with two rates of rumen cooling (Experiment XI)

Rumen infusion	Ambient temperature ($^{\circ}\text{C}$)	Feed intake level ($\text{g.kg LW}^{-0.75}.\text{day}^{-1}$)				
		20	35	55	80	110
HOT	+10	47	55	67	83	107
	-20	74	88	83	88	105
COLD	+10	51	59	68	86	103
	-20	73	105	123	122	131

Table 8.3 Ambient temperature and rumen infusion temperature interaction means for heat production (W.m^{-2}) of sheep (Experiment XI)

Ruminal infusion treatment	Ambient temperature ($^{\circ}\text{C}$)		Difference (-20 less +10)
	+10	-20	
HOT	71 ae	88 ae	17
COLD	74 ae	110 bf	36
(COLD-HOT)	3	28	

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

occurred at high ($+10^{\circ}\text{C}$) ambient temperatures. For a response to ruminal cooling at the high levels of feed intake, a lower T_a was required but the metabolic response was greater (40%). For example, at the 80 g feed intake level and the HOT (38°C) ruminal infusion, M increased by only $6 \text{ W}\cdot\text{m}^{-2}$ (7%); whereas with the COLD (2°C) infusion, M increased by $36 \text{ W}\cdot\text{m}^{-2}$ or 42% with the decline in T_a . This interaction of feed intake level, T_a and the heat of warming will be discussed in the next section.

9. THE HEAT OF WARMING FOOD - A PERSPECTIVE

9.1 Effective Rumen Cooling

In most previous discussions on the warming of food and water consumed at temperatures below body temperature, the heat of warming has been expressed either as a continuous effect over a 24 h period (see Blaxter, 1962) or considered to exist only over the eating/drinking period (Holmes, 1970). The evidence from the present studies suggests that neither of these two time bases is the most appropriate in defining the actual impact of the heat of warming.

The consumption of cold food or water in effect cools the *rumen* and the lowered rumen temperature may have an effect on the host animal. The rumen acts as an intermediate thermal pool between the cold food and the animal. The net rate of heat flow into the rumen from the body may reflect a more realistic estimate of the *effective* cooling of the animal per se, than HW expressed per 24 h or over the feeding period. If the net heat flow into the rumen was valuable in defining the actual cooling of the animal due to the consumption of cold feed, then it is important to quantify the *effective* rumen cooling (ERC) in response to varying amounts of HW and if possible provide a practical means for predicting ERC under field conditions. ERC can be considered as a total quantity of heat or as a

rate in a similar way to HW.

The consumption of cold high moisture feeds has two primary effects in the rumen as a consequence of the lowered temperature:

1. Direct stimulation of thermal sensors in the rumen and subsequently the body core which presumably induce the physiological and metabolic responses to cold. In this regard, the rumen and body act in concert. The sensation by the animal of the rumen cooling will likely be dependent on rumen temperature or rate of change of rumen temperature and would therefore probably follow a time course such as that depicted in Figure 4.1 (Experiment I, page 39).
2. Induction of a temperature gradient between the rumen and the deep body and thus a net flow of heat into the rumen. Heat flow from the body to the rumen not only depends on the temperature gradient between the body and the rumen (see Experiment II) but also on rumen volume and heat gained by the rumen from microbial fermentation in the rumen. In this context the body and the rumen contents can be considered as two separate heat pools.

,np> An estimate of the heat flow from the body to the rumen over the eating period was made in Experiment V (Table 6.8, page 113). Because of the potential significance of the

ERC, a further analysis of the rate of heat flow from the body into the rumen over the feeding and post-feeding periods was made using data from woolly sheep ruminally cooled during feeding, and in the absence of feeding (Experiment I). Details of the method of estimating heat flow into the rumen are given in appendix VIII and the results are shown on Figure 9.1. Points of interest from this analysis are:-

1. Heat flow from the body into the rumen was as great in the 30 min after rumen cooling stopped as in the first 30 min of rumen cooling.
2. Only 55 to 65% of the total heat flow into the rumen occurred during the actual rumen cooling phase.
3. 95% (NOT FED treatment) and 100% (FED treatment) of the net cooling of the rumen had been recovered by the rumen within 2 h post cooling.
4. When feeding accompanied cooling the heat flow from the body to the rumen was reduced by 20 to 40% and the rate of recovery post-cooling was more rapid. The contribution of fermentation heat production was equal to 30 to 40 kJ per MJ of digestible energy intake. Webster et al. (1975) estimated that over a 24 h period 30 to 60 kJ of fermentation heat were produced per MJ of digestible energy intake but did not give an hourly or diurnal breakdown of the fermentation heat production. The present estimation of the contribution of fermentation heat depends on

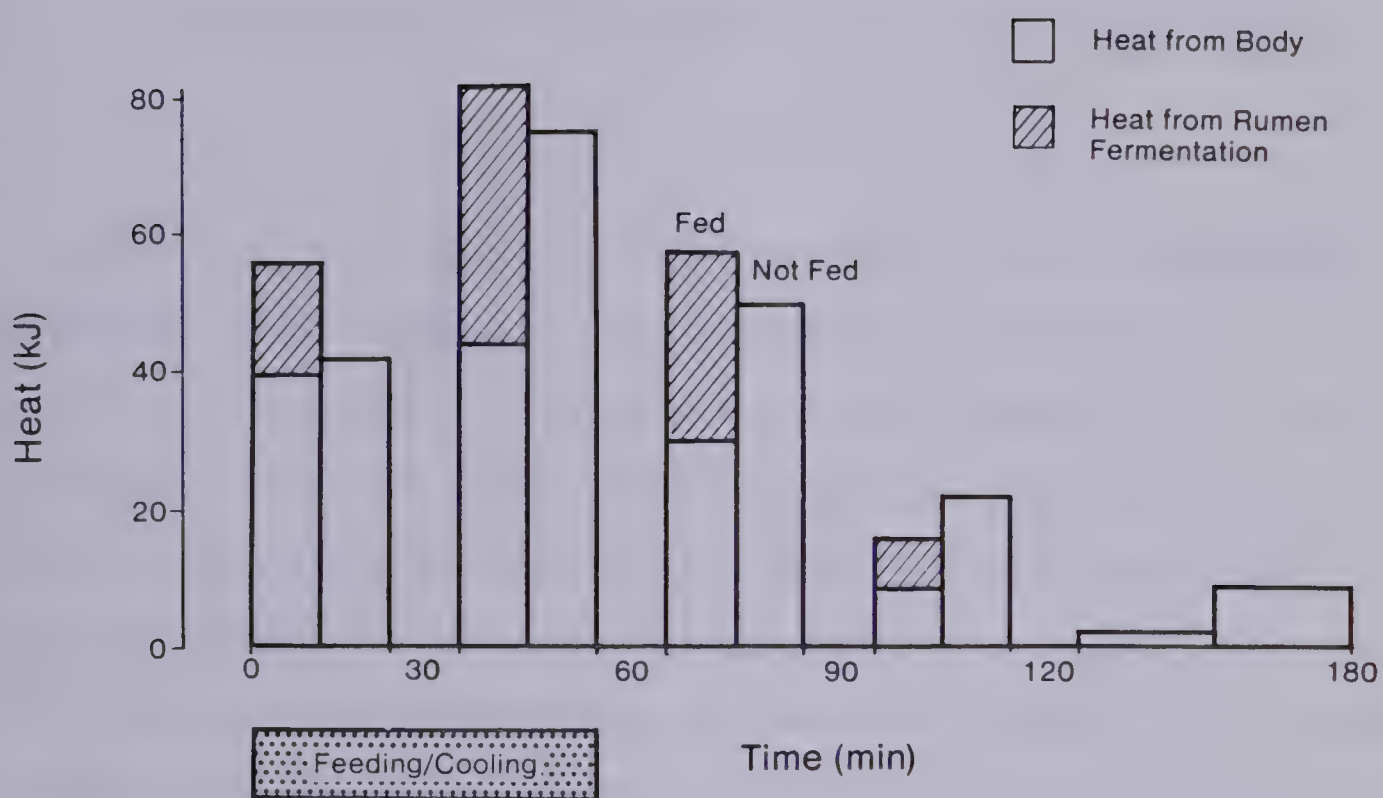


Figure 9.1 Heat flow into the rumen of sheep during and following 210 kJ of rumen cooling over 1 h (Experiment I)

assumptions of differences in the rumen volume of FED and NOT FED treatments and may tend to overestimate fermentation heat production during feeding and underestimate the contribution of fermentation heat during the immediate post-feeding period.

5. A heat flow into the rumen of a sheep of 80 kJ over one hour was equivalent to a heat flow of 140 W.m^{-2} of rumen surface area, about three times the minimum rate of heat loss from the external surface of the sheep.

The heat flow profile from the body into the rumen was dependent on HW (temperature, dry matter and quantity of food) and the amount of fermentation heat (quantity of food consumed). The heat flow from the body to the rumen over the hour of eating presented in Figure 9.1 and from Table 6.8 (Experiment V with cattle) was regressed against HW per unit of DE. The relationship is shown in Figure 9.2. As HW increased by 10 kJ per MJ DE intake the heat flow into the rumen as a percentage of DE intake increased by 0.56 percentage units.

In the Experiments used to establish the relationship in Figure 9.2, the rate of eating was 4 to 5 g dry matter.kg LW⁻¹.h⁻¹. The percentage of HW entering the rumen during the eating period depends on the rate of cooling/eating (Experiment II). The deviation from this model, representing a four-fold difference in cooling rate

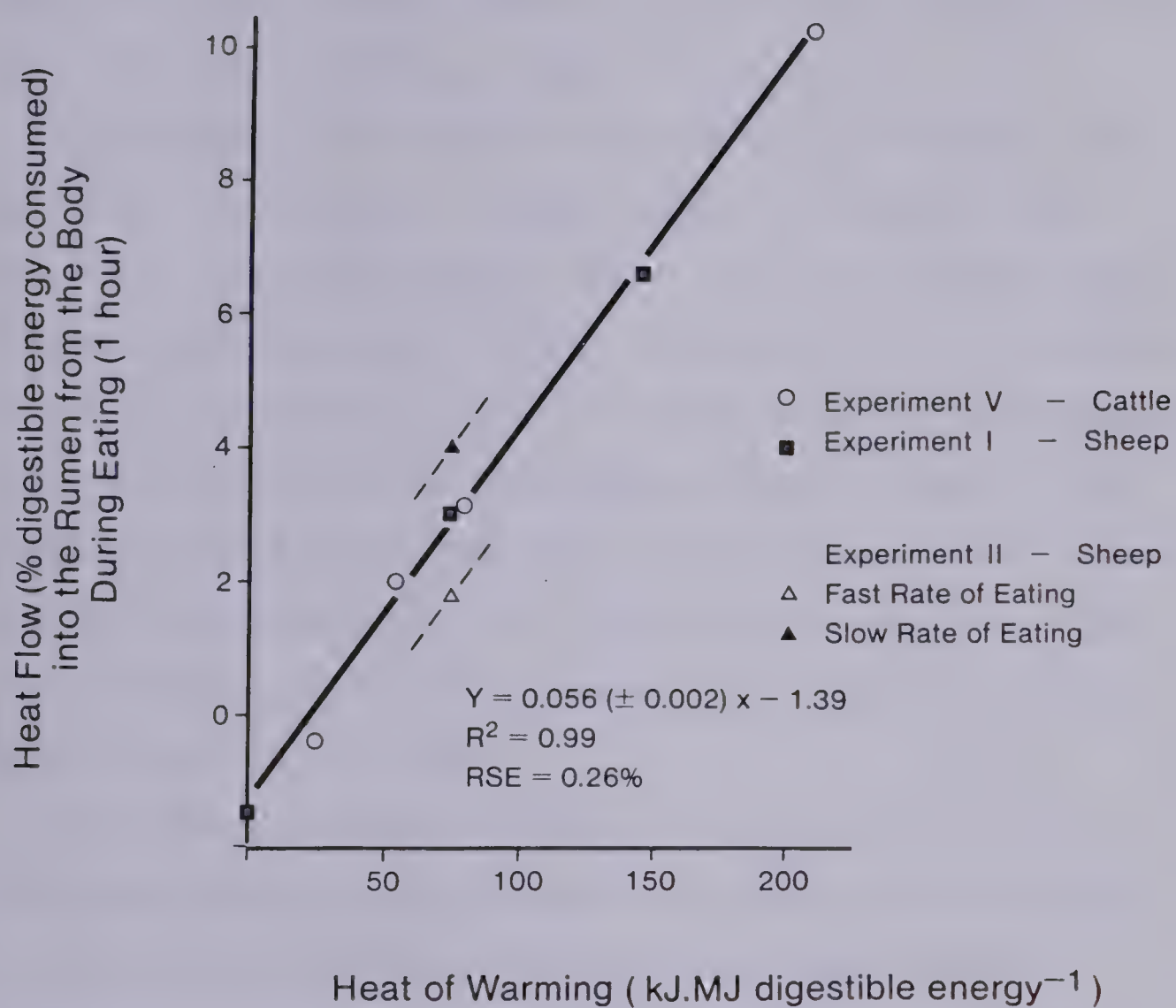


Figure 9.2 Relationship of heat flow into the rumen and rumen cooling per unit digestible energy intake (Experiments I, II and III solid line represents a rate of eating of 4 to 6 g dry matter per minute and broken line a four-fold range in the rate of eating)

(Experiment II), is also shown in Figure 9.2.

The heat flow into the rumen in the hour after cooling is approximately 50% of that during cooling (Figure 9.1) and the 'rate of cooling' limits would be reversed, with faster rates of rumen cooling inducing greater heat transfer into the rumen after cooling stopped.

A further simplification in defining the heat flow into the rumen from the body can be made if the assumption is made that all high moisture feeds have a dry matter content of 10% and a DE content of the dry matter of 14.5 MJ DE.kg DM⁻¹. Then for every °C that the temperature of the feed was below 33°C, 2 kJ of heat would move from the body to the rumen per kg of fresh feed eaten in one hour. With a feed temperature above 33°C, this relationship predicts a heat gain by the animal from the rumen as a result of microbial fermentation in the rumen.

Further refinement of the prediction of heat flow into the rumen would be possible with knowledge of the actual rates of eating, total time spent eating and rumen temperature changes associated with eating under field conditions.

9.2 A possible Heat of Warming model

The most common approach to predicting the influence of the environment on domestic species has been to estimate total heat loss from the physical heat exchange of the animal with the environment and to compare this loss with

the heat produced by the animal. If heat production exceeds the minimum, and does not exceed the maximum possible heat loss to the environment, then the environment is considered to have no net effect on the heat balance of the animal.

When the heat flow from the animal to the environment exceeds the heat generated in the animal, the animal increases heat production at the expense of energy conservation as tissue accretion in the body.

The conventional model (Monteith and Mount, 1974) showing the influence of ambient temperature on body heat loss is depicted in Figure 9.3a for a thermoneutral heat production of M_1 . Fasting heat production (FHP) representing minimum heat loss (H_{min}) is also shown. Critical body temperature (T_c) is the ambient temperature (or rather range of perhaps 5°C, Webster, 1974) below which no further reduction in heat loss can occur. The rate of increase in heat loss below T_c (line A in Figure 9.3a) is proportional to the total insulation of the body (tissue and external insulation). At an ambient temperature equal to body temperature the only source of heat loss is assumed to be the minimum evaporative heat loss.

The heat of warming has been incorporated into this model (Figure 9.3b). Effective rumen cooling is shown as an additional heat loss from the body (to the rumen, not to the external environment) which will raise the minimum heat loss of the animal at any T_a . This model in effect treats the rumen as a thermal sub-system within the total animal. The

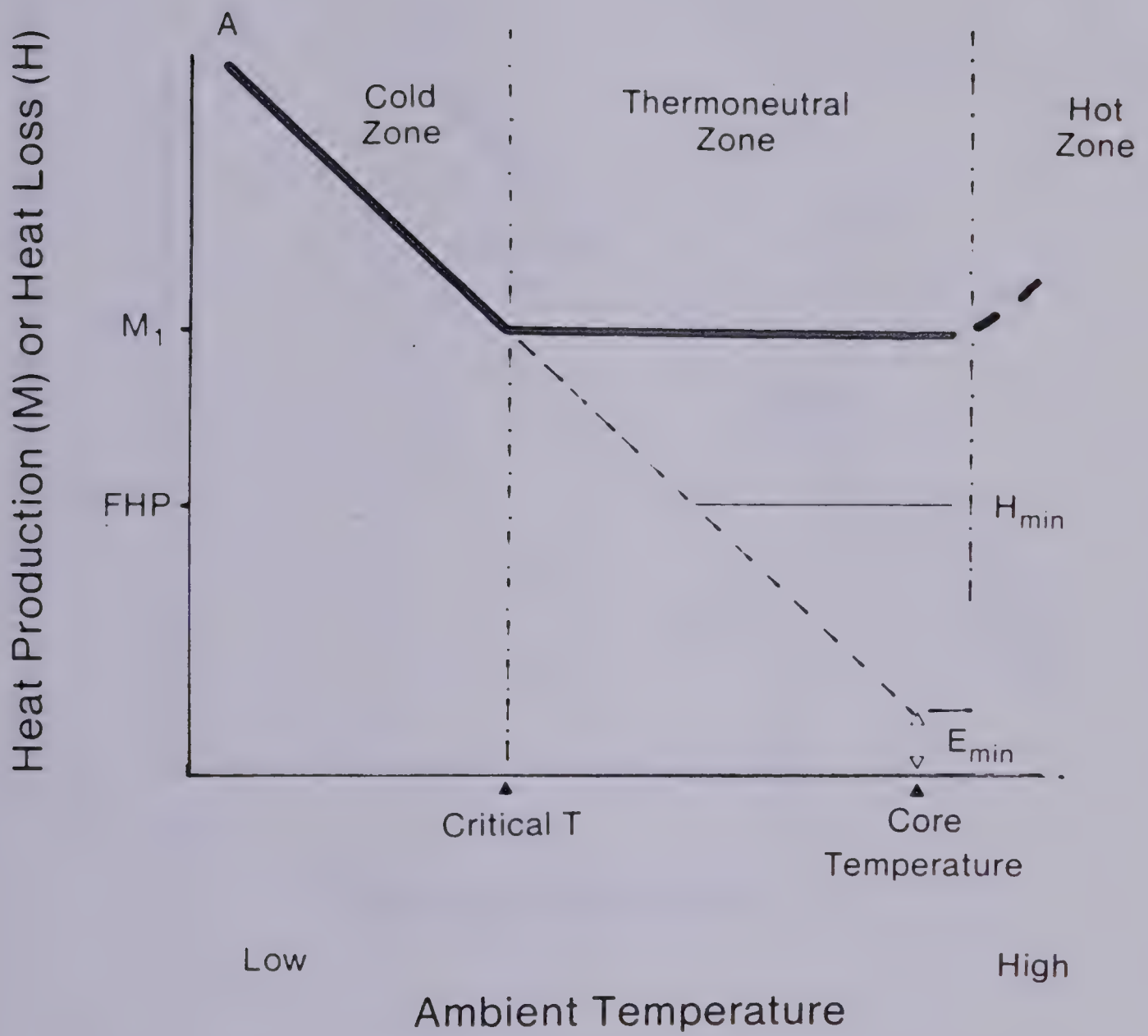


Figure 9.3a Relationship of heat loss of homeotherms with changes in ambient temperature

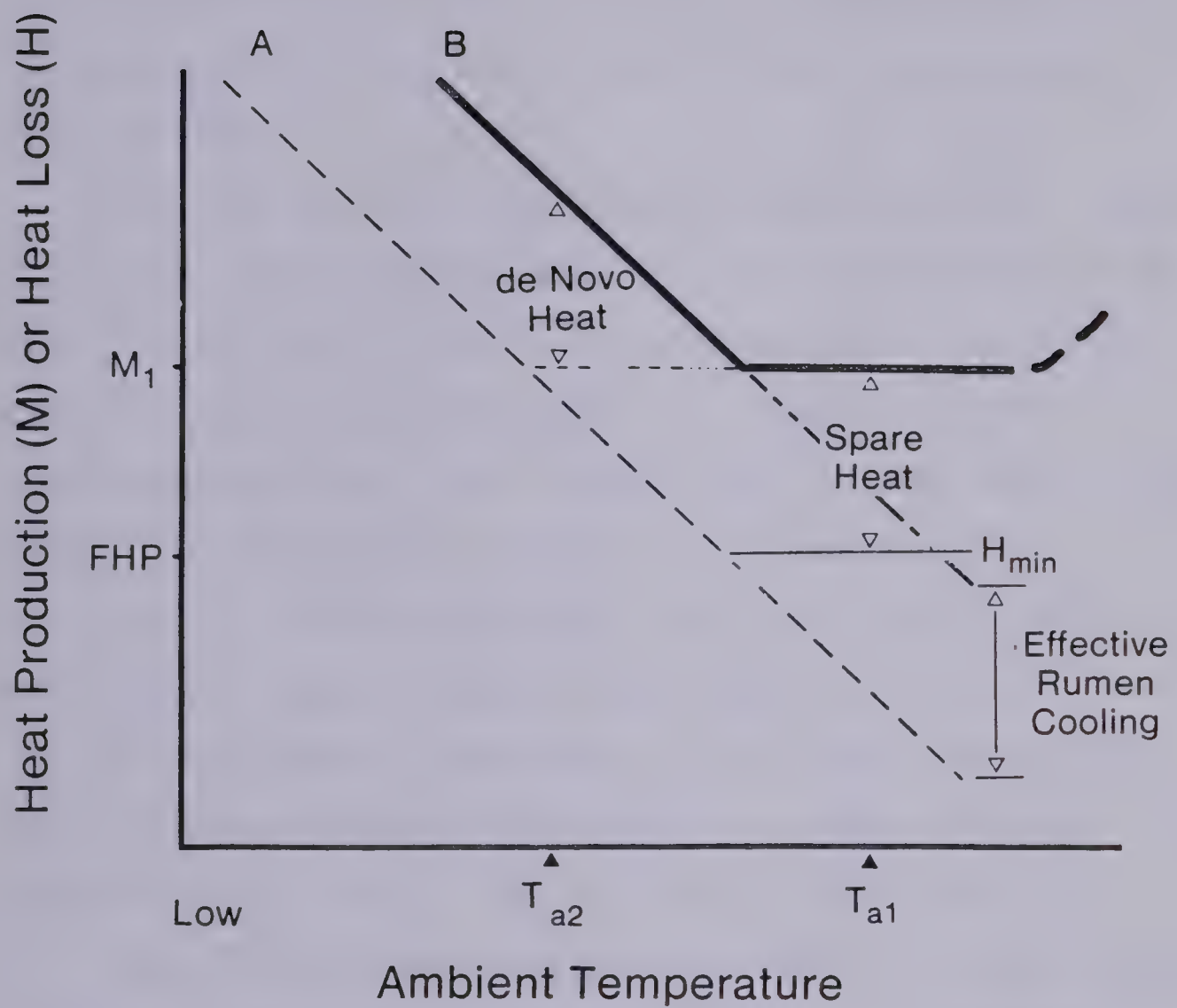


Figure 9.3b Heat loss model incorporating the heat of warming

actual displacement of the *effective* rumen cooling (ERC) from minimum heat loss (H_{min}) will be dynamic, moving from being no different from H_{min} when the rumen and body temperatures are equal (line A); following a time course profile determined by the rumen-body temperature gradient and returning to zero when rumen and body temperatures are again equalised.

With the level of heat production $M1$, shown on Figure 9.3b at an ambient temperature of $Ta1$, the *spare* heat ($M1 - H_{min}$) is sufficient to meet the ERC and the effect of ERC would simply be to reduce body heat loss (H) to the environment and body heat content (HC). *Spare* heat in this context is the extent to which H is above H_{min} , but in practice will include the heat available from a reduction in heat content (see discussion Experiment I).

At $Ta2$ however, *spare* heat is no longer adequate to meet the requirements of ERC and heat production must rise (*de novo* heat, line B, Figure 9.3b) to cover ERC.

Figure 9.4 shows the mean data and plot of the linear regressions calculated from the results of Experiment X where the heat production of steers was measured at three ambient temperatures. The solid line represents H_{min} in the absence of any rumen cooling and predicts that the fasting heat production (H_{min} in thermoneutrality, 70 W.m^{-2}) would occur at $+10^\circ\text{C}$. In Table 9.1a the calculated values of *spare* and *de novo* heat are compared with the heat of warming expressed in a number of ways (Experiment X). The following

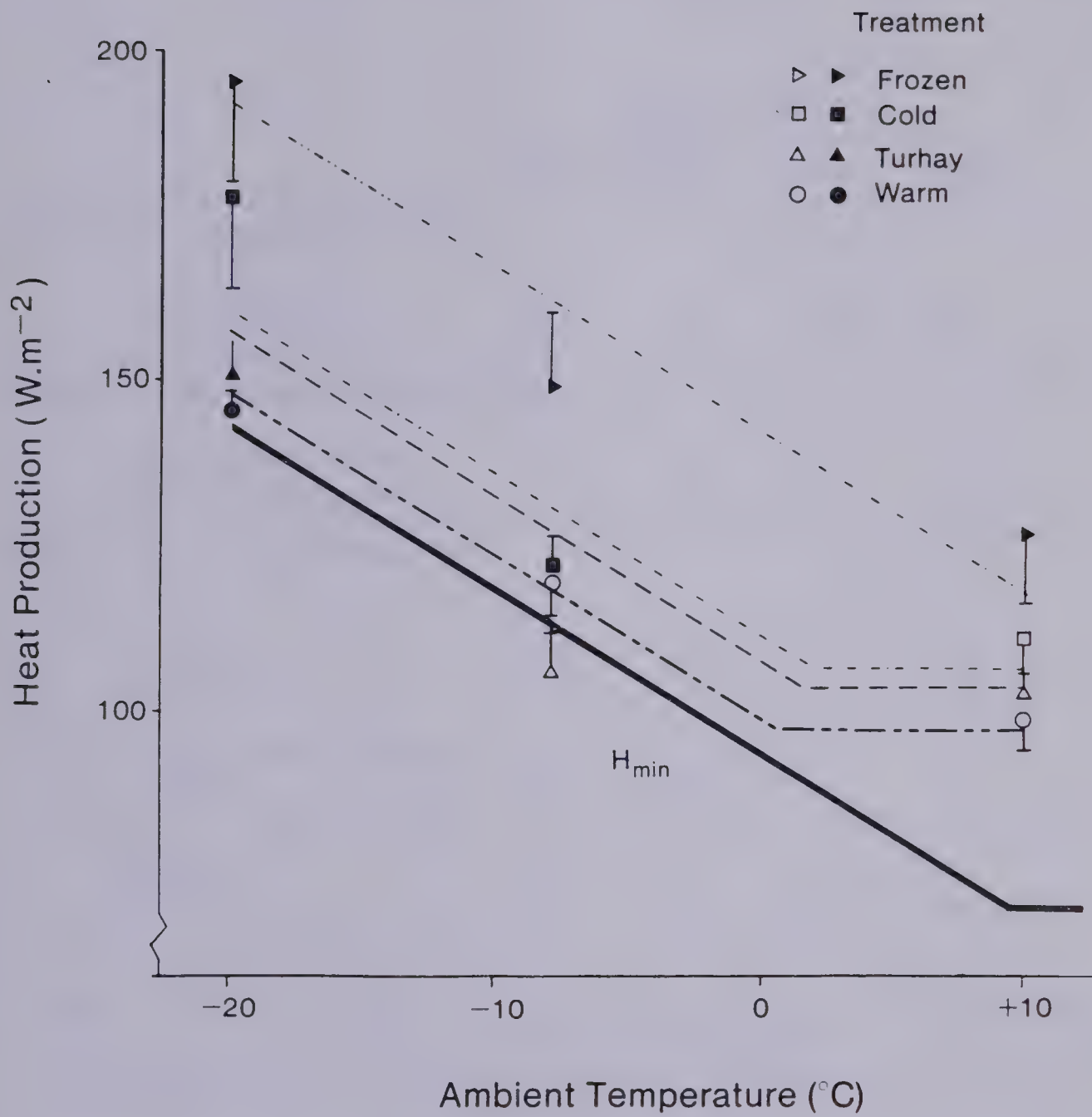


Figure 9.4 Heat production of steers at ambient temperatures of +10, -8 and -20°C (Experiment X) (solid symbols, heat production outwith thermoneutrality; open symbols within thermoneutrality)

Table 9.1a Comparison of the heat of warming with the effective rumen cooling, spare and de novo heat of cattle (Experiment X)

	Feed Treatment			
	WARM	TURHAY	COLD	FROZEN
Heat of Warming (W.m^{-2})				
mean daily ¹	3	7	9	25
during eating	30	87	105	295
Effective rumen cooling (W.m^{-2})				
by calculation ²	-5	8	11	43
from regression	5	14	17	48
Heat production (W.m^{-2})				
At +10°C				
spare ³	29	29	29	29
de novo	0	4	13	28
total heat above <i>H_{min}</i>	29	33	42	57
At -20°C				
spare	0	0	0	0
de novo	3	8	35	52

¹ mean daily = total HW per day expressed as a constant rate over the 24 h period
 during eating = Heat of warming per meal as a rate during eating (W.m^{-2})

² by calculation = calculated from rumen volume and temperatures
 from regression = predicted from the regression of HW on heat production (Experiment X)

³ spare = Heat production in thermoneutrality in excess of minimum heat loss
 de novo = Heat produced in response to ruminal cooling

Table 9.1b Comparison of the heat of warming with the effective rumen cooling, spare heat and de novo heat of sheep (Experiment XI)

	Feed intake (g.kg LW ^{-0.75} .day ⁻¹)				
	20	35	55	80	110
Heat of Warming (W.m ⁻²)					
mean daily ¹	5	8	13	18	24
during eating	23	33	52	73	98
Effective rumen cooling (W.m ⁻²)					
by calculation ²	7.5	12	17	25	34
Heat production (W.m ⁻²)					
At +10°C					
spare	3	13	25	40	64
de novo	5	4	1	4	-3
total heat above H _{min}	8	17	26	44	61
At -20°C					
spare	0	0	0	0	21
de novo	-2	17	40	32	27
total heat above H _{min}	-2	17	40	32	48

¹ mean daily = total HW per day expressed as a constant rate over the 24 h period
 during eating = Heat of warming per meal as a rate during eating(W.m⁻²)

² by calculation = from Table 7.2 and Figure 9.2

³ spare = Heat production in thermoneutrality in excess of minimum heat loss
 de novo = Heat produced in response to ruminal cooling

points can be noted:-

1. *Effective* rumen cooling calculated from rumen volume and rumen temperature data was similar to that statistically estimated from heat production data.
2. The predicted increase in *M* was more closely related to ERC than to HW expressed per day or per meal.
3. At 10°C, *spare* heat in theory should have been sufficient to cover ERC in all but the FROZEN treatment, but at least with the COLD treatment some *de novo* heat seems to have been produced.
4. At -20°C, no spare heat existed with any treatment and the actual increase in *M* over predicted *H_{min}* was similar to ERC calculated from rumen temperatures.

A similar exercise was carried out with sheep data from Experiment XI by comparing the difference in HW between the COLD and HOT treatments. Minimum heat production at +10°C was taken to be 42 W.m⁻² (Experiment VIII) and at -20°C to be the mean heat production of the 20, 35, 55 and 80 - HOT treatments. For this analysis, ERC was predicted from the HW for each feed intake and HW treatment (Table 7.2) and from the relationship between HW and DE intake (Figure 9.2). The results are shown in Table 9.1b. Again the actual response in heat production was more closely related to ERC than to other expressions of HW.

The analyses shown in Table 9.1a,b tend to substantiate the concept that *effective* rumen cooling may be a more precise definition of the actual cooling effect of HW.

Furthermore, the general model proposed to incorporate ERC appears to hold for the limited data available. If such a model proves tenable, many of the apparently conflicting responses to internal cooling obtained in these and other studies could be satisfactorily explained.

9.3 Efficiency of heat substitution

The total heat available, (spare plus de novo) to substitute for the cooling effect of HW is generally in excess of what was calculated to be moving into the rumen (Table 9.1a,b).

Values for spare and de novo heat and heat flows into the rumen were calculated indirectly and must therefore be subject to some error of estimation. However, the trend towards more heat being available than is required is quite consistent.

In the cattle experiment (Experiment X), where the data used involved the period immediately *after* cooling, the apparent over-supply of heat may represent the regain of previous heat content debt, although this is less likely to be a factor in the sheep data where actual feeding/cooling periods are included in the analysis.

It is possible that the efficiency of substituting heat from other sources towards warming the rumen to compensate for consuming cold feeds may not be 100%. For example, how effectively can heat produced during the synthesis of subcutaneous fat be directed into the rumen? Furthermore,

assumption of a 100% efficiency of substitution implies absolute control over heat loss and heat production.

Unless the consumption of cold feed and water was continuous, there will be periods of time where no body heat content debt exists and spare heat will be lost from the body only to be followed by a period of cooling where that heat could have been used for heating the rumen. Thus the profiles of availability and demand for spare heat are out of phase.

During rumen cooling experiments, considerable rumen and deep body cooling occurred *before* minimal skin temperatures were achieved. Thus the reduction in heat loss was not as effective in *saving* heat as would have been the case had skin temperatures fallen more rapidly.

There is also some speculative evidence that *de novo* heat was not used with 100% efficiency. In Experiment VIII the mean daily ear temperature of sheep at the lowest level of feed intake but receiving the coldest rumen infusion was higher than the ear temperature of sheep at the same intake but receiving the warm rumen infusion (Table 7.6, page 140). Also when HW was deducted from M of sheep at the lowest feed intake level, the residual level of heat production still *increased* as HW increased (Figure 7.3, page 138). Steers fed rations varying widely in HW (Experiment V) for two weeks prior to measuring body temperatures, tended to have higher prefeeding mean body temperatures when rations with a high HW were being fed. Webster (1978) has speculated that

additional heat produced to meet the demands of thermal stress from low ambient temperatures may not be 100%.

The data in Table 9.1a,b were used to calculate the apparent partial efficiencies of using spare and de novo heat for rumen warming. *Effective* rumen cooling was regressed against spare and de novo heat. The multiple regression was constrained through zero intercept. The partial efficiencies were 0.47 and 0.67 for spare (*ks*) and de novo (*kn*) heat respectively. Both regression coefficients were significant ($p < 0.05$) and the coefficient of determination (R^2) was 0.85.

The same exercise was repeated using total daily heat production and daily HW data from treatment combinations in Experiment VIII in which both spare and de novo heat were contributing to HW. The partial efficiencies of substitution were 0.50 and 0.37 for spare and de novo respectively. The efficiency of heat substitution might be anticipated to be lower in the second case, since the *daily* heat of warming was used. ERC was under-estimated by *daily* HW (Table 9.1), and thus efficiency of substitution would appear lower.

Thus possibly only 50% of spare heat is effectively channelled to warming the rumen contents, but when *M* is increased in response to rumen cooling then up to 70% of it is effectively used for warming the rumen. This conclusion must be tentative since it is likely that factors such as initial body heat content and daily ERC profile will

influence these efficiencies. The present data are not sufficiently diverse to permit much further analysis of factors affecting the efficiency of heat substitution. In any prediction of the possible increase in M due to the consumption of cold food or water correction for the possible inefficiencies of heat substitution would seem appropriate.

9.4 Habituation to the heat of warming

There was no evidence from the present work (Experiment V) that any permanent rise in metabolic rate occurred in response to repeated rumen cooling. Such an acclimation to exposure to low ambient temperatures for long periods of time (weeks) has been shown to occur in sheep (Webster et al., 1969; Sykes and Slee, 1969) and in beef cows (Young, 1975). Resistance to cooling may represent a reduction in available heat content buffer. On the other hand, the habituation of sheep to short cold shocks (2 h duration) on a daily basis reported by Slee (1972) in which a progressively greater decline in rectal temperature occurred may represent an increase in available heat content buffer. The existence of such a habituation to the heat of warming could be of value in reducing the impact of the heat of warming on metabolic rate. This possibility was not studied in these experiments but remains a topic for future consideration.

9.5 Other sources of heat

Experiments in this study were conducted with penned animals and therefore the level of physical activity was low. Under grazing conditions where physical activity levels are likely to be higher, there should theoretically be more spare heat available to substitute for the HW.

Hong and Nadel (1979) have shown that the increased heat production of exercising humans effectively substituted for an increase in M with declining ambient temperature. On the other hand, when sheep were fed during cold periods of the day there was no net reduction in total daily heat production compared with feeding during the warmer part of the day (Christopherson, 1974). The increased activity of the sheep during eating may have increased heat loss so that the potentially beneficial effect of the increase in heat production due to eating was lost. In Experiment I in the present study the increase in M measured during feeding did not appear to substitute for the increase in M induced by rumen cooling, although this result was confounded by the sporadic eating during a continuous cooling period. It is certainly unclear whether all sources of heat can effectively be used to meet the requirements of HW.

Figure 9.5 summarises the concepts of the heat of warming developed during this study. The heat required to warm the food and water consumed at temperatures below body temperature can be expressed per day or per meal, but the

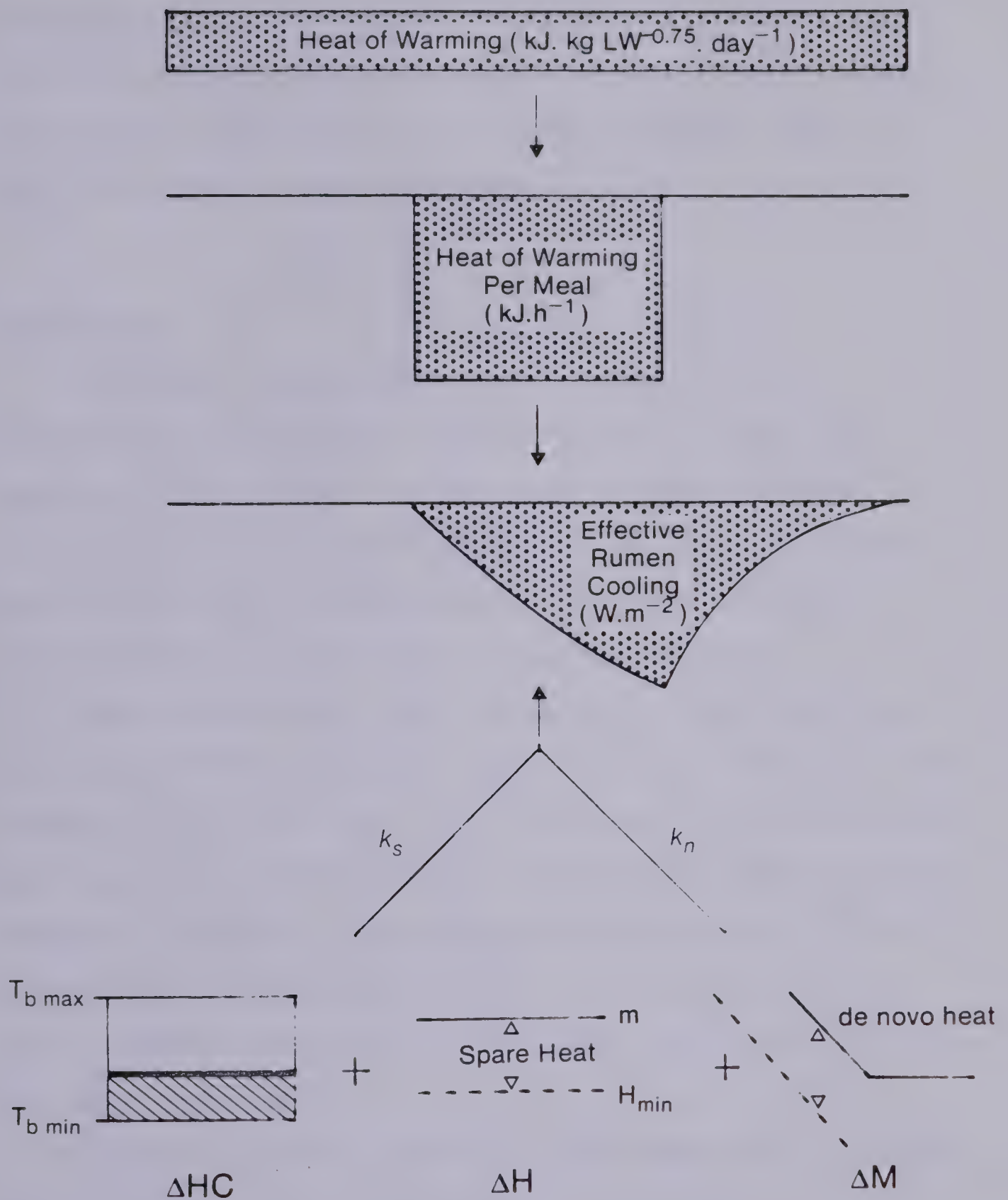


Figure 9.5 Summary of the effects of the heat of warming

better expression of the effect of cooling is the effective cooling profile in the rumen. Reduction in heat loss and body heat content plus an increase in heat production are utilised with efficiencies of k_s and k_n respectively to supply the heat to warm the rumen.

9.6 Summary

Analyses of the results from a number of the experiments in this study suggested that the rate and quantity of heat flow into the rumen (effective rumen cooling) was a more useful indication of the rate of body cooling due to the consumption of cold feed than HW expressed over the eating period or per 24 hours.

Experimental data reported in this study supported the inclusion of ERC as an additional source of heat loss from the body (but to the rumen, not to the external environment) which can be incorporated into conventional models of heat exchange in animals. The potential contribution of HW to thermal balance equations could thus be made relatively easily. More information on ERC under field conditions is obviously required.

Evidence presented suggested that body heat in excess of the minimal loss to the external environment can only substitute with an efficiency of 50% for HW whereas heat produced specifically in response to ruminal cooling may be used with an efficiency approaching 70%. If these calculations of efficiency of heat substitution are proved

correct, then a simple calculation of HW will underestimate the potential impact of HW on thermal balance.

10. CONCLUSIONS

The heat required to raise the temperature of ingested food and water to body temperature has generally been ignored as a component in the thermal balance of ruminants. However, practical field situations do exist where the heat of warming could play a significant role in the thermal economy and therefore productivity of domestic livestock. Such field situations are where large quantities of cool or cold high moisture feeds are consumed or where snow is a source of water.

A series of short-term trials (4 h duration) showed that there were three basic responses of the ruminant to the heat of warming cold food as simulated by ruminal cooling. These were

1. A reduction in heat loss (H) from the animal to the environment as demonstrated by a decline in skin temperatures (sensible heat loss) and reduced respiratory frequency (evaporative heat loss).
2. A reduction in total body heat content (HC) as witnessed by a drop in mean body temperature.
3. A rise in heat production (M). The reduction in heat loss and heat content may be insufficient to prevent an increase in metabolic rate.

The extent to which H , HC and M changed with rumen cooling and the relative contribution of the three components to the overall response was influenced not only by the quantity and rate of the rumen cooling but by the physiological state of the animal and the ambient temperature. Knowledge of the interaction between the animal and the effects of the heat of warming would allow the design of systems to minimise the likely impact of the heat of warming on productivity. For example, thermally stable i.e. large, well-insulated animals on a high plane of feed intake may tolerate large single meals of cold feed. On the other hand, smaller, poorly fed, poorly insulated stock may require feeding in small quantities over a longer time.

The majority of cooling from the consumption of cold feed occurred in the rumen. Heat transfer from the body to the mouth contributed only 5 to 10% of the total heat of warming of cold turnips fed to cattle. The profile of heat flow into the rumen from the body appeared to be a better definition of the effective cooling of the cold feed than the heat of warming expressed per day or per meal. Consequently, in field situations where the heat of warming may be of thermal importance, more information on the pattern of changes in rumen temperature and rumen volume is required.

In an energy balance study in which daily feed intake was supplied in six meals over an extended period (18 h),

metabolisable energy intake for maintenance was increased 24% when a simulated 10% dry matter feed was fed at 2°C in an ambient temperature of 10°C. Efficiency of utilisation of ME for maintenance was reduced with the cold feed, but the utilisation of metabolisable energy for positive energy retention was increased. Obvious care is required in interpreting efficiency of energy utilisation data if the heat of warming is of importance in thermal balance. There was no evidence in these experiments that the efficiency of digestion was significantly affected by the heat of warming although critical studies of digestion in the rumen and post-ruminal tract were not carried out.

If the rumen is treated as a separate thermal source from the host animal, the heat flow from the body into the rumen can be treated as a source of heat loss from the animal and as such be incorporated into conventional models of heat exchange between the animal and its environment. Prediction of the change in critical temperature and the relative sensitivity of animals to changes in ambient temperature and the heat of warming are possible.

From the data available from this study, it would seem that excess body heat (heat above minimal heat loss) cannot be used very efficiently for warming the rumen. Part of the inefficiency of heat substitution lies in the relatively constant supply but fluctuating demand for this heat. While this imperfect phasing of supply and demand can be partly tempered by the body heat content buffer, the buffering

capacity itself is limited by physiological limits of temperature regulation. Furthermore, in situations where HW is likely to be large, (low ambient temperatures) the HC content buffer is low, and when HC is high, HW is less likely to be as large.

On the basis of these studies it would seem prudent to include the heat of warming ingested feed and water in models predicting the effect of the environment on physiological and metabolic functions, feed requirements and animal productivity.

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APPENDIX Ia EXPERIMENT I

Treatment by time period interaction means for main treatment effects (Experiment I)

Treatment	Period				Treatment mean	±SEM
	I	II	III	IV		
Heart rate (beats.min ⁻¹)						
INFUSION	78.8	88.9	95.6	78.9	83.1	1.53
COIL	75.2	91.2	88.7	76.6	83.1	
NIL	78.5ae	88.0ae	78.9ae	75.8ae	80.3	1.88
LOW	76.4ae	90.1be	84.7abe	76.6ae	82.0	
HIGH	76.1ae	92.2be	97.8bf	80.9ae	86.8	
FED	76.6ae	102.1cf	93.2bf	83.1af	88.8e	1.53
NOT FED	77.4abe	78.1abe	81.1be	72.4ae	77.3f	
Period means	77.8a	90.1b	87.1b	77.8a		1.18
Urine output (ml.min ⁻¹)						
INFUSION	4.3ae	14.5ae	55.5be	55.7be	32.5e	1.44
COIL	5.7ae	6.8ae	6.9af	5.3af	6.2f	
NIL	5.0	9.8	28.8	31.4	18.8	0.96
LOW	5.7	10.9	25.6	26.6	17.1	
HIGH	4.1	11.2	39.3	33.8	22.1	
FED	5.4	9.2	27.7	25.4	17.0e	1.44
NOT FED	4.5	12.0	34.7	35.5	21.7f	
Period means	5.0a	10.6ab	31.2 b	30.5b		1.71
Rectal temperature (°C)						
INFUSION	38.9	38.7	38.6	38.8	38.8	0.05
COIL	38.8	38.6	38.6	38.8	38.7	
NIL	38.8ae	38.9ae	39.0ae	39.0ae	38.9e	0.06
LOW	38.8ae	38.6abf	38.5bf	38.8ae	38.7ef	
HIGH	38.9ae	38.5bcf	38.3bcf	38.7abf	38.6f	
FED	38.9	38.7	38.7	38.9	38.8	0.05
NOT FED	38.8	38.6	38.5	38.8	38.7	
Period means	38.9a	38.7b	38.6c	38.8a		0.02

Treatment	Period				Treatment mean	±SEM
	I	II	III	IV		
Ear skin temperature (°C)						
INFUSION	28.3	25.2	20.1	19.9	23.4	1.3
COIL	25.2	24.3	21.9	20.7	23.0	
NIL	24.0ae	26.2ae	26.7ae	25.6ae	25.6	1.7
LOW	27.8ae	25.3abe	19.6bf	18.6bcf	22.8	
HIGH	28.5ae	22.7ae	16.7bf	16.7bf	21.2	
FED	24.5ae	23.7ae	22.3ae	22.0ae	23.1	1.7
NOT FED	29.0ae	25.8ae	19.8be	18.6be	23.3	
Period means	26.8a	24.7a	21.0b	20.3b		0.7
Leg skin temperature (°C)						
INFUSION	27.5	24.5	21.5	21.5	13.7e	1.2
COIL	23.0	20.2	17.8	18.6	19.9f	
NIL	24.4ae	23.4ae	23.4ae	24.5ae	23.9	1.5
LOW	24.9ae	21.7abe	18.8abf	20.1abf	21.4	
HIGH	26.4ae	21.9ae	16.5cf	15.7cg	20.1	
FED	24.2	21.6	19.3	20.4	21.4	1.2
NOT FED	26.2	23.1	19.8	19.8	22.2	
Period means	25.2	22.3	19.5	20.2	21.8	1.5
Trunk skin temperature (°C) two sheep only						
INFUSION	33.9	34.4	34.2	34.0	34.1	0.2
COIL	34.3	34.6	34.8	34.6	34.6	
NIL	33.5	33.8	35.4	34.6	34.3	0.3
LOW	34.7	34.8	34.1	34.3	34.4	
HIGH	34.2	34.9	34.1	34.0	34.3	
FED	34.0	34.6	34.4	34.5	34.4	0.2
NOT FED	34.2	34.4	34.6	34.1	34.3	
Period means	34.1	34.5	34.5	34.1		0.3

Treatment	Period				Treatment mean	±SEM
	I	II	III	IV		
Rumen temperature (°C) on dorsal sac (two sheep)						
INFUSION	39.1	37.6	38.2	38.9	38.4	
COIL	39.0	37.1	37.8	38.9	38.2	0.14
NIL	39.1ae	38.9ae	39.2ae	39.1ae	39.1e	
LOW	39.0ae	36.7cf	37.8bf	38.9ae	38.1f	
HIGH	39.1ae	36.4bf	37.0bg	38.7ae	37.8f	0.17
FED	39.1	37.9	38.4	39.1	39.1e	
NOT FED	39.0	37.1	37.6	38.7	38.1f	0.14
Period means	39.1a	37.4c	38.0b	38.9a		0.08

Rumen temperature (°C) in dorsal sac						
INFUSION	39.2	36.2	37.8	38.9	38.0	
COIL	39.0	35.5	36.9	38.9	37.6	0.16
NIL	39.1ae	39.0ae	39.3ae	39.2ae	39.1e	
LOW	39.0ae	34.4cf	37.2bf	38.8ae	37.4f	
HIGH	39.1ae	34.1bf	35.5bg	38.6ae	36.8f	0.19
FED	39.1	36.2	37.9	39.1	38.1e	
NOT FED	39.1	35.5	36.8	38.6	37.5f	0.16
Period means	39.1a	35.8c	37.3b	38.9a		0.16

Rumen temperature (°C) on ventral sac						
INFUSION	38.9	37.9	38.2	38.7	38.4	
COIL	38.8	37.2	37.6	38.6	38.1	0.20
NIL	38.9ae	38.9ae	38.9ae	38.9ae	38.9e	
LOW	38.8ae	37.0bf	37.7bf	38.5ae	38.0f	
HIGH	38.9ae	36.7bf	37.0bf	38.5ae	37.8f	0.24
FED	38.9	37.8	38.4	38.9	38.5	
NOT FED	38.8	37.2	37.4	38.4	38.0	0.20
Period means	38.9a	37.5b	37.9b	38.7a		0.14

Treatment	Period				Treatment mean	±SEM
	I	II	III	IV		
Rumen temperature (°C) in ventral sac						
INFUSION	38.8ae	36.6ce	37.6be	38.6ae	37.9	0.13
COIL	38.9ae	35.5cf	37.1be	38.7ae	37.6	
NIL	38.8ae	38.9ae	39.0ae	39.0ae	38.9e	0.16
LOW	38.9ae	35.7cf	37.3bf	38.7ae	37.4f	
HIGH	38.9ae	33.6bcf	35.7bg	38.3ae	36.6g	
FED	38.8	36.3	37.9	39.0	38.0e	0.13
NOT FED	38.9	35.8	36.8	38.3	37.5f	
Period means	38.9a	36.1c	37.3b	38.7a		0.12
Rumen temperature (°C) core						
INFUSION	39.1ae	36.9be	38.1be	38.9ae	38.2e	0.13
COIL	39.0ae	34.2cf	37.9be	39.0ae	37.5f	
NIL	39.0ae	38.8ae	39.3ae	39.3ae	39.1e	0.16
LOW	38.9ae	35.6bf	37.8af	38.9af	37.8f	
HIGH	39.2ae	32.1cg	36.9bg	38.6af	36.7g	
FED	39.1	35.9	38.2	39.2	38.1e	0.13
NOT FED	39.0	35.2	37.8	38.7	37.7f	
Period means	39.0a	35.5c	38.0b	38.9a		0.19
Oxygen consumption (ml.min ⁻¹)						
INFUSION	217	227	231	215	222	5
COIL	202	219	235	204	215	
NIL	217ae	223ae	219ae	206ae	217	6
LOW	208ae	225abe	235ef	213ae	221	
HIGH	204ae	221ae	245bf	206ae	219	
FED	211ae	233be	252ce	225be	229e	5
NOT FED	209abe	213bf	213bf	194af	206f	
Period means	211a	223b	233c	208a		2

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

Appendix Ib

Sample example of the statistical model used in Experiment I
 Analysis of variance for rectal temperature

Source	DF	Sum of squares	Mean square	F ratio
Sheep	2	0.4259	0.2130	1.41
Method of cooling	1	0.0711	0.0711	0.47
Level of cooling	2	2.7172	1.3586	9.03
Fed vs Not fed	1	0.6400	0.6400	4.25
Method x level	2	0.7622	0.3811	2.53
Method x fed	1	0.0028	0.0028	0.002
Level x fed	2	3.1017	0.0508	0.337
Error (a)	24	3.612	0.1515	
Periods	3	1.4581	0.4860	21.65
Method x period	3	0.0794	0.0264	1.17
Level x period	6	2.3111	0.3851	17.16
Fed x period	3	0.0083	0.0028	0.124
Error (b)	93	2.0881	0.02245	

Means for three sheep for all treatment effects at 10 min intervals during the 4 h trials (Experiment I)

Heart Rate (beats.min⁻¹)Urine output ($\text{ml} \cdot \text{min}^{-1}$)Rectal temperature (°C).

Method of cooling (line 1, INFUSION; line 2, COIL)																						
38.8	38.8	38.8	38.8	38.9	38.9	38.9	38.8	38.8	38.7	38.6	38.5	38.6	38.6	38.6	38.6	38.6	38.8	38.8	38.6	38.8	38.8	38.9
38.8	38.8	38.9	38.8	38.8	38.8	38.8	38.8	38.8	38.7	38.5	38.5	38.5	38.6	38.6	38.6	38.7	38.7	38.8	38.8	38.8	38.8	38.8
Level of cooling treatment (line 1, NIL; line 2, LOW; line 3, HIGH)																						
38.8	38.8	38.8	38.8	38.8	38.8	38.9	38.9	38.9	38.9	39.0	39.0	39.0	39.0	39.0	39.0	39.0	38.8	39.0	39.0	39.0	39.0	39.0
38.9	38.8	38.8	38.8	38.9	38.9	38.9	38.8	38.7	38.7	38.5	38.5	38.5	38.6	38.6	38.6	38.6	38.7	38.8	38.8	38.8	38.8	38.8
38.8	38.8	38.9	38.9	38.9	38.9	38.9	38.9	38.8	38.6	38.4	38.3	38.1	38.2	38.2	38.2	38.3	38.4	38.4	38.6	38.7	38.8	38.8
FED versus NOT FED treatment (line 1, FED; line 2, NOT FED)																						
38.9	38.9	38.9	38.9	38.9	38.9	38.9	38.8	38.8	38.7	38.6	38.6	38.7	38.7	38.7	38.7	38.7	38.8	38.7	38.9	39.0	39.0	39.0
38.8	38.8	38.8	38.8	38.8	38.8	38.8	38.8	38.8	38.7	38.5	38.5	38.5	38.6	38.6	38.6	38.6	38.7	38.7	38.7	38.7	38.7	38.8

Appendix Ic continued

Ear temperature (°C)

Method of Cooling (line1, INFUSION; line 2, COIL)											
25.5	27.3	27.8	28.2	28.5	28.7	29.0	28.5	27.7	26.5	25.0	22.6
22.7	24.3	24.7	25.3	25.7	25.7	25.8	26.6	26.1	24.2	23.0	23.0
Level of Cooling (line 1, NIL; line 2, LOW; line 3, HIGH)											
21.7	22.5	22.8	23.7	24.3	25.0	25.3	26.5	26.4	26.2	26.4	26.4
25.8	27.6	27.6	27.9	28.1	27.8	28.0	27.8	27.4	26.3	25.2	23.3
24.9	27.4	28.3	28.6	28.9	28.7	28.8	28.3	26.9	23.6	20.6	18.8
FED versus NOT FED (line 1, FED; line 2, NOT FED)											
21.4	23.3	24.0	24.7	25.2	24.9	25.1	25.0	25.0	24.1	23.5	22.5
26.8	28.4	28.6	28.8	29.0	29.4	29.7	30.0	28.8	26.6	24.5	23.2

Leg temperature (°C)

Method of Cooling (line1, INFUSION; line 2, COIL)											
27.6	27.7	27.8	27.6	27.4	27.1	27.1	26.5	25.9	24.9	23.9	23.3
22.9	23.2	23.6	23.2	22.8	22.8	22.5	22.0	21.4	20.3	19.4	19.0
Level of Cooling (line 1, NIL; line 2, LOW; line 3, HIGH)											
24.7	24.7	24.6	24.3	24.2	24.3	24.0	23.6	23.5	23.4	22.9	23.4
25.0	25.4	25.4	25.3	24.8	24.6	24.3	23.7	23.0	22.1	21.2	20.4
26.0	26.3	27.0	26.7	26.3	26.0	26.1	25.4	24.3	22.4	20.9	19.7
FED versus NOT FED (line 1, FED; line 2, NOT FED)											
24.2	24.3	24.8	24.5	24.1	23.9	23.7	23.2	22.6	21.9	21.1	20.6
26.3	26.6	26.5	26.4	26.1	26.0	25.8	25.3	24.6	23.4	22.3	21.8

Rumen temperature (°C) - on dorsal sac

Method of Cooling (line1, INFUSION; line 2, COIL)											
39.0	39.1	39.0	39.0	39.1	39.1	39.1	38.7	38.0	37.6	36.7	37.3
38.9	39.0	39.0	39.0	39.0	39.0	39.0	38.4	37.7	37.2	36.8	36.3
Level of Cooling (line 1, NIL; line 2, LOW; line 3, HIGH)											
39.0	39.1	39.0	39.0	39.1	39.1	39.1	39.1	39.0	39.1	38.0	39.1
38.9	38.9	38.9	38.9	38.9	39.0	38.9	38.1	37.1	36.5	36.4	36.1
39.0	39.0	39.0	39.1	39.1	39.1	39.1	38.6	37.5	36.6	35.8	35.2
FED versus NOT FED treatment (line 1, FED; line 2, NOT FED)											
39.0	39.0	39.0	39.1	39.1	39.1	39.1	38.5	37.9	37.5	37.4	37.3
38.9	39.0	39.0	39.0	39.0	39.0	39.0	38.6	37.9	37.3	36.1	36.3

Appendix Ic continued

Rumen temperature (°C) - in dorsal sac

Method of Cooling (line1, INFUSION; line 2, COIL)

39.1	39.1	39.2	39.2	39.2	39.1	37.3	36.2	35.9	35.8	35.8	35.9	36.5	37.2	37.8	38.1	38.4	38.6	38.7	38.8	38.9	39.0	39.0
38.9	39.0	39.0	39.1	39.1	39.0	37.9	36.3	35.4	34.7	34.7	34.7	34.1	34.7	35.9	36.8	37.5	38.0	38.4	38.6	38.8	38.9	39.0
Level of Cooling (line 1, NIL; line 2, LOW; line 3, HIGH)																						
39.0	39.1	39.1	39.2	39.2	39.1	39.0	38.9	39.0	39.0	39.0	39.0	39.1	39.2	39.2	39.2	39.3	39.3	39.2	39.2	39.2	39.2	39.1
39.0	39.0	39.0	39.1	39.1	39.0	36.6	34.7	34.0	33.7	33.8	33.8	33.8	35.1	36.4	37.3	37.8	38.2	38.5	38.6	38.8	38.9	39.0
39.0	39.1	39.1	39.2	39.2	39.1	37.2	35.2	34.0	33.1	32.9	32.9	32.1	32.4	34.1	35.2	36.3	37.2	37.8	38.1	38.4	38.5	38.9
FED versus NOT FED treatment (line 1, FED; line 2, NOT FED)																						
39.0	39.1	39.1	39.2	39.2	39.1	37.5	36.4	36.0	35.8	36.0	36.0	35.7	36.4	37.2	37.8	38.4	38.7	38.9	39.0	39.1	39.2	39.2
39.0	39.0	39.1	39.1	39.1	39.0	37.7	36.1	35.3	34.8	34.5	34.5	34.3	34.8	36.0	36.7	37.2	37.8	8.1	38.3	38.5	38.6	38.7

Rumen temperature (°C) - on ventral sac

Method of Cooling (line1, INFUSION; line 2, COIL)

38.8	38.8	38.9	38.9	38.9	38.9	38.6	38.1	37.8	37.7	37.5	37.5	37.5	37.8	38.0	38.1	38.3	38.4	38.5	38.6	38.6	38.7	38.7
38.7	38.8	38.8	38.9	38.9	38.8	38.4	37.7	37.1	36.9	36.5	36.5	36.4	36.7	37.2	37.5	37.8	38.0	38.3	38.4	38.5	38.6	38.7
Level of Cooling (line 1, NIL; line 2, LOW; line 3, HIGH)																						
38.8	38.8	38.9	38.9	38.9	38.9	38.9	38.8	38.8	38.8	38.9	38.9	39.0	38.9	39.0	39.0	38.9	38.9	38.9	38.9	38.9	38.8	38.8
38.7	38.7	38.8	38.8	38.8	38.8	38.0	37.4	36.9	36.9	36.5	36.5	36.5	36.9	37.4	37.7	38.0	38.1	38.3	38.4	38.5	38.6	38.7
38.8	38.9	38.9	39.0	39.0	39.0	38.6	37.4	36.6	36.1	35.7	35.7	35.3	35.9	36.4	36.8	37.2	37.5	37.9	38.2	38.3	38.5	38.6
FED versus NOT FED treatment (line 1, FED; line 2, NOT FED)																						
38.9	38.9	38.9	38.9	38.9	38.9	38.5	37.9	37.7	37.7	37.5	37.5	37.5	37.8	38.1	38.3	38.5	38.6	38.7	38.8	38.9	38.9	38.9
38.7	38.8	38.8	38.8	38.8	38.8	38.9	38.5	37.9	37.2	36.9	36.6	36.4	36.7	37.0	37.3	37.6	37.8	38.0	38.2	38.3	38.4	38.5

Rumen temperature (°C) - in ventral sac

Method of Cooling (line1, INFUSION; line 2, COIL)

38.8	38.8	38.9	38.9	38.9	38.8	38.9	37.7	37.1	36.7	36.4	36.4	36.5	36.8	37.2	37.6	38.0	38.2	38.4	38.5	38.5	38.6	38.7
38.7	38.7	38.8	38.9	38.9	38.9	38.8	37.6	36.0	34.9	34.1	33.7	33.4	34.8	36.0	37.0	37.6	38.0	38.2	38.4	38.5	38.6	38.7
Level of Cooling (line 1, NIL; line 2, LOW; line 3, HIGH)																						
38.8	38.8	38.9	38.9	38.9	38.9	38.8	38.8	38.8	38.8	38.9	38.9	39.0	39.0	39.0	39.0	39.0	39.0	39.0	38.9	38.9	38.9	38.9
38.6	38.7	38.7	38.8	38.8	38.7	38.8	36.9	35.1	34.6	34.7	34.2	34.5	35.7	36.6	37.2	37.7	38.0	38.2	38.3	38.5	38.6	38.7
38.8	38.8	38.9	38.9	38.9	38.9	39.0	37.2	35.8	34.0	32.3	31.9	31.4	32.6	34.1	35.6	36.6	37.3	37.6	37.9	38.2	38.3	38.6
FED versus NOT FED treatment (line 1, FED; line 2, NOT FED)																						
38.7	38.8	38.8	38.9	38.9	38.9	37.5	36.5	35.6	35.3	35.2	35.2	35.3	36.1	37.2	37.8	38.2	38.5	38.7	38.7	38.9	38.9	39.0
38.7	38.8	38.8	38.9	38.9	38.8	38.9	37.8	36.6	36.1	35.2	34.8	34.6	35.4	36.0	36.7	37.3	37.7	37.9	38.1	38.2	38.3	38.4

Appendix 1c continued

Rumen temperature (°C) - core

Method of Cooling (line1, INFUSION; line 2, COIL)														
38.9	39.0	39.0	39.1	39.2	39.1	37.9	37.2	36.9	36.4	36.3	36.5	37.2	37.7	38.0
38.9	39.0	39.0	39.0	39.0	38.7	35.4	34.9	33.5	33.8	33.5	33.8	36.5	37.6	37.9
Level of Cooling (line 1, NIL; line 2, LOW; line 3, HIGH)														
38.8	38.9	38.9	39.0	39.0	39.0	38.5	38.8	38.9	38.9	39.0	39.0	39.2	39.3	39.3
38.9	38.9	39.0	39.0	39.1	38.6	36.7	36.5	35.1	34.9	34.9	35.2	36.5	37.3	37.7
39.0	39.1	39.1	39.2	39.2	39.1	34.7	32.8	31.7	31.6	30.8	31.1	34.9	36.4	36.9
FED versus NOT FED treatment (line 1, FED; line 2, NOT FED)														
38.9	39.0	39.0	39.1	39.1	39.1	36.5	36.2	35.5	35.7	35.5	35.6	37.0	37.9	38.2
38.9	39.0	39.0	39.0	39.0	38.7	36.7	35.9	34.9	34.6	34.2	34.6	36.8	37.4	37.8

Oxygen consumption (ml.min⁻¹)

Method of Cooling (line1, INFUSION; line 2, COIL)														
222	217	224	215	210	215	220	225	225	231	234	243	238	235	225
202	204	205	205	204	194	205	208	209	216	244	256	250	239	228
Level of Cooling (line 1, NIL; line 2, LOW; line 3, HIGH)														
221	220	220	213	212	213	222	222	224	220	223	222	215	217	216
212	208	216	209	204	202	214	218	220	224	242	253	249	237	226
202	203	207	208	205	198	202	210	207	219	238	271	269	257	237
FED versus NOT FED treatment (line 1, FED; line 2, NOT FED)														
208	208	211	212	212	210	217	227	229	234	245	264	258	264	251
215	213	218	208	202	199	209	206	206	208	218	234	230	210	202

Temperature of the room (°C)

Method of Cooling (line1, INFUSION; line 2, COIL)														
9.5	9.6	9.7	9.7	9.9	9.9	10.1	10.2	10.3	10.2	10.2	9.6	10.1	10.0	10.0
8.8	9.0	9.1	9.3	9.4	9.7	10.0	9.9	10.0	10.1	10.3	10.3	9.9	9.7	9.7
Level of Cooling (line 1, NIL; line 2, LOW; line 3, HIGH)														
9.1	9.1	9.2	9.4	9.5	9.6	10.1	10.0	10.0	10.1	9.9	10.1	9.8	9.7	9.7
9.1	9.3	9.4	9.4	9.6	9.7	10.0	10.1	10.2	10.2	10.3	10.0	10.0	9.9	9.9
9.4	9.5	9.7	9.7	9.8	10.1	10.1	10.2	10.2	10.2	10.3	9.7	10.3	9.9	9.9
FED versus NOT FED treatment (line 1, FED; line 2, NOT FED)														
9.1	9.2	9.2	9.2	9.4	9.6	9.9	9.9	10.0	10.1	10.2	9.7	10.1	9.9	9.9
9.3	9.5	9.6	9.8	9.9	9.9	10.2	10.3	10.2	10.3	10.1	10.2	9.9	9.8	9.8

Appendix II Experiment II

Treatment by period interaction means for all variables

Treatment	Period				Treatment means	SEM
	I	II	III	IV		
Heart rate (beats.min ⁻¹)						
SLOW	78	88	77	73	79	
MED	78	89	89	77	81	
FAST	86	93	80	77	84	3.1
DURING	72ae	97be	81ae	77ae	81	
POST	90bcf	84bcf	77abe	74ae	81	2.6
Period means	81a	90b	79a	76a		1.4
Rectal temperature (°C)						
SLOW	39.0ae	39.0ae	38.9abef	38.9ae	39.0	
MED	39.0ae	38.9abe	38.7bf	38.9abe	38.9	
FAST	39.0ae	38.9be	39.0abe	39.1af	39.0	0.08
DURING	38.9ae	38.9ae	38.9ae	39.1bf	38.9	
POST	39.1af	39.0abe	38.9be	38.9be	39.0	0.07
Period means	39.0a	38.9a	38.9b	39.0a		0.02
Ear skin temperature (°C)						
SLOW	30.9	30.9	26.8	24.4	28.3	
MED	26.7	26.0	20.5	22.6	24.0	
FAST	29.8	24.3	17.7	23.1	23.7	2.7
DURING	26.1	24.4	20.3	22.5	23.3	
POST	32.2	29.7	23.1	24.2	27.3	2.2
Period mean	29.2a	27.1a	21.7b	23.4b		1.0
Leg skin temperature (°C)						
SLOW	25.2ae	23.9abe	22.0abe	20.5be	22.9	
MED	20.4ae	20.8ae	19.7ae	20.9ae	20.5	
FAST	21.8ae	20.7ae	20.4ae	24.6ae	21.9	2.8
DURING	21.0	18.9	18.7	20.8	19.9	
POST	23.9	24.7	22.7	23.2	23.6	2.3
Period means	22.5	21.8	20.7	22.0		0.5

Treatment	Period				Treatment means	SEM
	I	II	III	IV		
Trunk skin temperature (°C)						
SLOW	34.5	34.5	34.6	34.8	34.6	0.5
MED	34.4	34.3	34.1	34.4	34.3	
FAST	34.5	34.3	34.3	34.6	34.4	
DURING	34.1	34.1	34.1	34.5	34.2	0.4
POST	34.9	34.7	34.5	34.7	34.7	
Period means	34.5	34.4	34.3	34.6		0.1
Rumen core temperature (°C)						
SLOW	39.5ae	37.8be	36.8be	38.8ae	38.5	0.14
MED	39.4ae	36.4cf	38.1bf	39.5ae	38.4	
FAST	39.5ae	35.9bf	39.1af	39.6af	38.5	
DURING	39.2ae	36.5ce	38.2be	39.4ae		0.11
POST	39.8af	36.9ce	37.8be	39.1ae	38.4	
Period means	39.5a	36.7c	38.0b	39.3a		0.12
Oxygen consumption (ml.min ⁻¹)						
SLOW	211ae	223ae	229ae	221ae	221	5.0
MED	204ae	229be	223abe	215abe	217	
FAST	245af	252af	235ae	231ae	239	
DURING	208ae	231be	239bf	225abe	227	3.0
POST	231abf	239be	219ae	219ae	227	
Period means	219a	235b	229ab	221a		3.0

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

Appendix IIb

Means for three sheep for all variables at 10 min intervals (Experiment II)

The first 6 values in each line are for the pre-treatment period, followed by 6 values over the treatment period (II) and a further 12 values over the recovery phase (Periods III and IV)

Heart rate(beats.min⁻¹)

Rate of cooling treatment (line 1, SLOW; line 2, MED; line 3, FAST)																					
83	78	81	74	75	78	85	88	89	91	89	80	78	75	74	78	75	76	73	71	71	70
80	81	80	78	74	74	84	87	89	91	90	94	86	81	74	75	76	81	79	76	73	73
86	93	90	83	87	78	88	90	97	94	97	94	81	82	77	79	78	74	75	80	75	77
Time of cooling treatment (line 1, DURING; line 2, POST)																					
69	74	72	71	74	68	87	95	98	98	103	100	85	84	78	77	76	79	78	75	75	74
96	94	95	85	83	84	84	82	86	84	82	85	79	78	73	75	78	75	76	73	73	73

Rectal temperature (°C)

Rate of cooling treatment (line 1, SLOW; line 2, MED; line 3, FAST)																					
39.0	39.0	39.0	39.0	39.0	39.0	39.0	39.0	39.1	39.0	39.0	39.0	39.0	38.9	38.9	38.9	38.9	38.9	38.9	39.0	38.9	39.0
38.8	38.9	38.9	38.9	39.0	39.0	39.0	39.0	38.9	38.9	38.8	38.8	38.7	38.7	38.7	38.7	38.8	38.8	38.9	38.9	39.0	39.0
38.9	38.9	38.9	39.0	39.0	39.0	39.0	39.1	39.0	38.9	38.8	38.8	38.9	39.0	38.9	39.0	39.1	39.0	39.2	39.1	39.1	39.1
Time of cooling treatment (line 1, DURING; line 2, POST)																					
38.8	38.8	38.8	38.9	38.9	38.9	38.9	38.9	39.0	38.9	38.8	38.8	38.9	38.9	38.9	38.9	39.0	39.1	39.1	39.1	39.0	39.1
39.0	39.0	39.1	39.1	39.1	39.1	39.2	39.1	39.1	39.0	38.9	38.9	38.9	38.8	38.9	38.9	38.9	38.9	38.9	39.0	39.0	39.0

Ear skin temperature (°C)

Rate of cooling treatment (line 1, SLOW; line 2, MED; line 3, FAST)																							
25.6	29.4	30.9	31.0	31.2	31.4	31.3	31.3	31.2	31.3	30.9	31.4	29.6	29.0	27.8	27.4	26.8	25.5	24.4	24.1	23.7	23.9	24.0	24.2
22.3	24.7	25.1	27.2	26.8	28.3	28.4	28.2	27.3	26.6	25.6	24.8	23.6	21.9	20.9	20.4	20.2	19.8	19.8	19.8	19.9	19.8	22.8	24.7
25.6	28.0	29.8	30.1	30.0	30.5	3	0.5	30.3	28.3	26.1	22.8	19.9	18.3	17.9	17.8	17.4	17.8	18.1	19.9	20.7	20.9	21.9	24.1
Time of cooling treatment (line 1, DURING; line 2, POST)																							
21.5	23.5	25.2	26.6	26.4	27.6	27.5	27.2	26.2	25.1	23.7	22.7	21.7	21.3	20.7	20.3	19.9	19.6	19.6	19.5	20.1	20.4	22.3	24.0
27.6	31.3	32.0	32.3	32.2	32.5	32.6	32.6	31.6	30.9	29.2	28.0	26.0	24.6	23.7	23.2	23.0	22.4	21.9	23.1	22.8	22.7	23.5	24.7

Leg skin temperature (°C)

Rate of cooling treatment (line 1, SLOW; line 2, MED; line 3, FAST)																							
23.7	24.3	24.5	25.5	25.7	25.7	25.3	24.0	24.6	24.5	23.6	23.3	23.6	22.7	22.2	21.8	21.8	21.4	21.7	20.5	19.5	19.8	20.7	20.7
20.5	20.2	20.1	19.9	20.5	20.6	21.1	21.2	21.5	21.3	21.2	20.0	19.7	19.3	19.3	19.5	19.8	20.3	20.1	19.8	20.3	20.4	21.2	21.8
20.5	20.9	20.9	21.3	22.7	22.5	22.3	22.6	21.3	20.2	20.4	19.9	20.0	19.6	18.9	19.9	20.9	20.8	22.1	22.6	23.6	23.9	24.4	25.8
Time of cooling treatment (line 1, DURING; line 2, POST)																							
20.4	20.9	20.5	20.7	21.6	21.5	20.9	19.9	19.5	19.0	18.9	18.2	18.1	18.0	17.9	18.3	19.0	19.1	19.5	19.2	19.1	19.9	21.5	22.1
22.8	22.7	23.1	23.9	24.4	24.5	24.9	25.3	25.4	25.0	24.6	23.9	24.1	23.1	22.4	22.6	22.6	22.6	23.1	22.8	23.2	22.9	22.7	23.5

Appendix IIc continued

Trunk skin temperature (°C)

Rate of cooling treatment (line 1, SLOW; line 2, MED; line 3, FAST)											
34.0	34.4	34.2	35.1	34.8	34.7	34.7	34.3	35.2	34.6	34.6	34.6
33.7	34.0	34.1	34.2	33.9	34.7	35.1	34.6	34.9	34.4	34.1	34.2
34.7	34.4	34.2	34.2	34.8	34.5	34.8	34.7	34.3	34.2	34.3	34.1
Time of cooling treatment (line 1, DURING; line 2, POST)											
33.9	33.9	34.1	34.8	34.2	33.9	33.9	34.0	34.5	34.0	34.1	33.8
34.4	34.6	34.3	34.3	34.8	35.4	35.8	35.1	35.2	34.8	34.6	34.4

Rumen core temperature (°C)

Rate of cooling treatment (line 1, SLOW; line 2, MED; line 3, FAST)											
39.3	39.4	39.5	39.6	39.7	39.7	39.5	38.2	38.0	37.9	37.4	37.6
39.2	39.2	39.3	39.4	39.4	39.5	39.4	37.7	37.4	36.3	36.0	35.9
39.3	39.4	39.5	39.6	39.6	39.7	39.0	36.7	34.3	33.4	35.9	37.2
Time of cooling treatment (line 1, DURING; line 2, POST)											
39.1	39.1	39.2	39.3	39.3	39.2	39.0	37.5	36.1	35.4	35.9	37.0
39.5	39.6	39.7	39.8	39.9	40.0	39.6	37.6	37.0	36.3	37.0	36.8

Oxygen consumption (ml.min⁻¹)

Rate of cooling treatment (line 1, SLOW; line 2, MED; line 3, FAST)											
200	206	213	212	215	212	210	220	222	224	234	233
192	204	205	210	202	212	220	226	210	235	237	248
248	243	238	239	254	245	252	254	242	247	259	250
Time of cooling treatment (line 1, DURING; line 2, POST)											
205	210	211	209	204	212	215	220	214	235	248	252
221	225	227	232	243	233	240	247	236	236	238	235

Appendix IIIa Experiment III

Feed Intake and insulation treatment by period
interaction means for all variables (Experiment III)

Treatment	Period				Treatment means	?SEM
	I	II	III	IV		
Heart rate (beats.min ⁻¹)						
WOOLLY-LOW	54ae	85be	68ae	62ae	67e	
WOOLLY-HIGH	87af	100bf	87af	83af	89f	
SHORN-HIGH	98ag	130bg	125bg	104ag	114g	1.7
Period means	80a	105c	93b	83a		1.7
Rectal temperature (°C)						
WOOLLY-LOW	38.7	38.7	38.4	38.5	38.6e	
WOOLLY-HIGH	38.9	39.0	38.8	38.8	38.9e	
SHORN-HIGH	38.2	38.1	38.1	38.1	38.1f	0.09
Period means	38.6a	38.6a	38.4b	38.5ab		0.04
Ear skin temperature (°C)						
WOOLLY-LOW	19.8	23.7	20.0	18.9	20.6e	
WOOLLY-HIGH	34.0	29.8	21.3	26.8	28.0f	
SHORN-HIGH	20.9	16.9	16.7	16.1	17.6e	1.45
Period means	24.9	23.5	19.3	20.6		1.50
Leg skin temperature (°C)						
WOOLLY-LOW	16.9	15.4	13.3	12.3	14.5e	
WOOLLY-HIGH	26.8	22.4	19.9	20.9	22.5f	
SHORN-HIGH	17.4	15.7	13.9	12.8	14.9e	0.85
Period means	20.4a	17.8ab	15.7b	15.4b		0.69

Treatment	Period				Treatment means	SEM
	I	II	III	IV		
Trunk skin temperature (°C)						
WOOLLY-LOW	33.9	33.2	33.9	34.0	33.7a	
WOOLLY-HIGH	31.2	30.8	30.9	31.1	31.0ab	
SHORN-HIGH	27.3	27.2	27.2	27.3	27.2b	0.13
Period means	30.8	30.4	30.7	30.8		0.13

Rumen core temperature (°C)						
WOOLLY-LOW	38.6	35.7	36.3	38.1	37.2	
WOOLLY-HIGH	39.1	36.3	36.5	38.8	37.7	
SHORN-HIGH	38.7	35.6	36.9	35.8	37.4	0.41
Period means	38.8a	35.9b	36.6b	38.5a		0.25

Oxygen consumption (ml.min ⁻¹)						
WOOLLY-LOW	170	198	204	188	190e	
WOOLLY-HIGH	249	276	254	252	258e	
SHORN-HIGH	337	409	405	337	373f	18.0
Period means	252a	295b	289b	260a		7.0

a,b,c,d means in rows followed by the same letter are not significantly different ($p < 0.05$)

e,f,g,h means in columns followed by the same letter are not significantly different ($p < 0.05$)

Means for two sheep for all variables over 10 min intervals (Experiment III)

The first 6 values on each line are over the pre-treatment period (I), the following six over the treatment period (II) and the final 12 values over the recovery phase (Periods III and IV)

Heart rate (beats.min⁻¹)

External insulation-feed intake treatment (line 1, GOOD-LOW; line 2, GOOD-HIGH; line 3, POOR-GOOD)

55	59	53	53	54	53	83	85	90	88	85	83	73	67	71	65	67	63	62	61	61	61	62	65
88	92	88	86	84	83	95	100	102	104	96	103	89	85	89	89	89	85	90	81	80	84	80	83
100	100	99	99	97	94	119	119	120	129	145	148	145	136	127	118	114	109	106	107	105	104	104	100

Rectal temperature (°C)

38.6	38.6	38.7	38.7	38.8	38.7	38.8	38.8	38.8	38.8	38.6	38.7	38.6	38.5	38.4	38.3	38.3	38.4	38.4	38.5	38.5	38.5	38.6	38.6
38.8	38.8	38.8	38.9	39.0	39.0	39.1	39.1	39.0	39.1	39.0	38.9	38.8	38.7	38.7	38.7	38.7	38.7	38.8	38.8	38.8	38.9	39.0	39.0
38.2	38.2	38.2	38.2	38.2	38.2	38.2	38.3	38.2	38.1	38.1	38.1	38.1	38.1	38.0	38.1	38.1	38.2	38.1	38.1	38.1	38.1	38.1	38.1

Ear skin temperature (°C)

16.5	17.8	18.7	19.5	19.9	21.0	22.1	25.8	25.3	24.8	23.4	22.1	21.1	20.8	20.3	20.0	19.8	19.6	19.4	18.6	19.1	18.9	18.8	18.9
33.6	34.2	33.6	33.8	34.5	33.9	34.2	33.7	33.1	31.0	28.9	26.9	25.5	23.3	21.8	21.0	20.3	20.0	21.5	23.7	25.0	26.3	28.2	28.8
22.8	23.0	22.8	22.0	20.4	19.0	18.2	17.3	17.2	17.3	17.3	14.9	17.3	17.0	16.7	16.6	16.6	16.5	16.3	16.3	16.1	16.2	15.8	15.9

Leg skin temperature (°C)

18.3	17.6	16.9	16.6	16.6	17.0	16.8	16.2	15.8	15.6	15.1	15.4	14.2	14.2	13.7	13.2	13.2	12.7	12.7	12.5	12.1	12.2	12.4	12.4
25.1	25.8	26.8	27.9	27.8	26.8	25.6	24.0	23.1	22.6	22.1	21.5	21.0	19.3	19.8	20.3	20.1	20.1	20.0	21.1	21.0	19.8	21.8	21.8
17.4	17.7	17.7	17.5	17.3	17.0	16.9	16.6	16.2	15.8	15.5	15.2	14.9	14.4	14.1	13.9	13.8	13.5	13.4	13.3	12.9	12.6	12.8	12.8

Trunk skin temperature (°C)

34.3	34.3	34.4	34.4	34.4	34.5	34.5	34.4	34.4	34.3	34.4	34.6	34.4	34.4	34.4	34.3	34.3	34.3	34.3	34.3	34.3	34.4	34.4	34.4
32.5	32.2	32.3	32.4	33.4	34.0	32.8	32.2	31.7	31.5	31.6	31.6	31.9	32.6	32.4	32.0	32.7	32.4	32.1	32.2	32.1	32.0	32.5	32.6
28.3	28.2	28.2	28.1	28.1	28.0	27.9	28.4	28.5	28.4	28.4	28.3	28.3	28.4	28.4	28.5	28.5	28.5	28.5	28.5	28.5	28.5	28.5	28.6

Rumen core temperature (°C)

38.5	38.5	38.6	38.6	38.6	38.7	38.7	36.6	35.4	35.0	34.7	34.1	34.1	35.5	36.6	37.0	37.4	37.5	37.7	38.0	37.9	38.1	38.3	38.5
38.9	39.0	39.1	39.1	39.2	39.2	39.2	37.3	36.5	35.7	34.5	34.6	33.0	35.6	36.6	37.5	38.0	38.3	38.5	38.6	38.8	38.8	39.0	39.0
38.7	38.7	38.8	38.7	38.8	38.8	38.3	36.8	35.7	34.6	33.8	34.4	35.2	36.3	37.0	37.4	37.6	37.9	38.2	38.3	38.4	38.6	38.7	38.7

Oxygen consumption (ml.min⁻¹)

165	176	168	171	172	165	187	179	190	202	221	211	211	211	202	208	200	201	197	185	184	182	189	194
251	253	249	245	243	252	269	281	276	282	279	273	261	260	255	248	249	248	251	244	245	253	258	257
326	339	346	343	332	342	359	360	375	413	464	487	465	467	397	377	370	355	337	346	350	341	337	320

Appendix IV Experiment IV

Time spent eating, feed eaten and oxygen consumption prior to, during and after eating five feed types

		Period	Eating time (min)	Feed eaten (kg fresh wt.)	Oxygen consumption (ml.min ⁻¹ , over 10 min periods)	
					Pre-feeding	Post-feeding
WHOLE TURNIPS						
Sheep 1	II	am	25.0	1.20	266 266 248 243	294 279 255 279
		pm	15.5	1.00	286 294 275 258	317 301 305 307
Sheep 2	IV	am	15.8	1.15	275 283 288 298	304 287 288 285
		pm	18.0	1.00	299 287 294 282	322 313 219 305
Sheep 3	III	am	12.5	0.70	237 253 256 253	290 288 270 272
		pm	8.0	0.40	265 256 257 240	282 288 262 264
Sheep 4	I	am	17.0	0.40	232 214 228 210	242 233 235 233
		pm	14.0	0.50	253 251 249 238	283 266 269 280
SLICED FRESH TURNIPS						
Sheep 1	I	am	24.0	1.30	220 244 237 237	309 282 296 275
		pm	26.0	1.20	249 251 239 235	309 288 270 268
Sheep 2	II	am	19.5	1.20	282 296 314 310	366 345 352 370
		pm	19.0	1.10	315 336 343 325	318 343 343 311
Sheep 3	IV	am	13.5	0.30	263 276 274 263	277 253 256 249
		pm	20.0	0.30	280 283 280 274	310 296 320 298
Sheep 4	III	am	22.0	0.80	231 225 228 228	265 257 257 254
		pm	13.0	0.25	230 233 231 245	251 256 270 280
FROZEN SLICED TURNIPS						
Sheep 1	IV	am	21.3	1.00	252 265 265 242	262 325 294 291
		pm	24.5	1.60	242 236 245 232	362 316 293 310
Sheep 2	III	am	25.0	1.30	293 293 296 290	290 367 353 322
		pm	22.0	0.80	348 338 338 338	364 353 355 360
Sheep 3	I	am	21.5	0.80	263 270 230 260	362 324 328 322
		pm	13.0	1.21	270 274 281 278	623 552 461 422
Sheep 4	II	am	23.0	0.30	269 258 249 239	273 253 230 242
		pm	25.0	0.40	212 205 205 215	233 229 236 240

Appendix IV continued

Time spent eating, feed eaten and oxygen consumption prior to, during and after eating (continued)

Period		Eating time (min)	Feed eaten (kg fresh wt.)	Oxygen consumption (ml.min ⁻¹ , over 10 min periods)			
				Pre-feeding		During feeding Post-feeding	
RATION A (concentrate pellet)							
Sheep 1	III	am	11.0	0.75	295 293 312 302	438 ---	387 397 396 390
		pm	11.3	0.75	305 300 292 300	389 ---	367 357 365 343
Sheep 2	I	am	6.0	0.75	354 354 352 336	450 ---	490 463 439 421
		pm	7.2	0.75	359 359 346 359	448 ---	432 439 432 436
Sheep 3	II	am	8.3	0.64	322 337 332 342	431 ---	416 407 400 387
		pm	11.5	0.34	332 339 324 322	397 ---	377 377 363 367
Sheep 4	IV	am	11.3	0.30	297 318 303 277	334 ---	332 323 305 312
		pm	10.0	0.20	280 283 280 274	329 ---	310 296 320 298
Additional data for LONG HAY							
Sheep 1	V	am	21.5	0.25	330 323 321 322	439 478	366 336 333 330
Sheep 2	V	am	21.0	0.121	292 306 328 315	434 426	341 309 304 327
Sheep 3	V	am	23.0	0.18	271 269 250 235	340 360	286 282 282 289
Sheep 4	V	am	21.0	0.07	265 250 243 250	349 365	280 276 276 276

Appendix V Experiment V Means over 30 min for all variables
Each value is the mean of four steers

Pre-feeding		During feeding		After eating			
WARM turnip treatment							
Rectal temperature (°C)							
37.9	38.1	38.2	38.3	38.4	38.4	38.4	38.5
38.1	38.2	38.2	38.1	38.1	38.1	0	0
Jugular temperature (°C)							
37.8	37.7	38.2	38.2	37.9	37.9	37.8	37.8
37.7	37.7	38	37.9	37.9	37.9	0	0
Ear skin temperature (°C)							
27.1	27.1	25.6	28.3	31.7	33.2	32.9	33.3
30.3	30	28.1	29.6	29.5	32.3	0	0
Leg skin temperature (°C)							
24.1	23.4	22.1	21.1	24.2	23.3	24	25.3
24.5	24.5	24.1	24	25.2	25.5	0	0
Trunk skin temperature (°C)							
26.1	27	26.6	26.2	26.5	26.1	27	27
27.5	26.4	27.1	27	27.6	26.9	0	0
Rumen core temperature (°C)							
37.8	38.6	38.4	38.7	38.9	39.5	39.7	39.5
39.3	39.1	38.9	39	39.7	40.2	0	0
Oxygen consumption (litres.h ⁻¹)							
1.02	1.02	1.43	1.6	1.4	1.2	1.2	1.14
1.2	1.21	1.57	1.73	1.48	1.35	0	0

TURHAY treatment

Rectal temperature (°C)							
38	38	37.9	38	38.2	38.2	38.3	38.4
38.3	38.4	38.4	38.3	38.4	38.4	0	0
Jugular temperature (°C)							
37.4	37.3	37.2	37.5	37.4	37.6	37.5	37.6
37.7	37.7	37.7	37.7	37.7	37.8	0	0
Ear skin temperature (°C)							
27.6	27.7	26.1	24.3	26.4	26	29.9	30.3
25.9	26.3	23.6	25.3	26.7	28.1	0	0
Leg skin temperature (°C)							
23.4	22.6	20.9	19.3	19.8	19.1	20.8	23
23.1	25.8	24.6	25	26	26.4	0	0
Trunk skin temperature (°C)							
28.5	28.2	27.7	27.4	28.1	27.6	27	27.8
25.8	26.8	26.4	19.9	20	19.9	0	0
Rumen core temperature (°C)							
38.1	38.3	37	37.1	37.8	38.5	39.3	39.3
38.9	39	38	37.8	38.5	39	0	0
Oxygen consumption (litres.h ⁻¹)							
1.13	1.05	1.46	1.67	1.3	1.29	1.36	1.26
1.18	1.21	1.59	1.67	1.41	1.37	0	0

Pre-feeding		During feeding		After eating			
COLD turnip treatment							
Rectal temperature (°C)							
38.6	38.7	38.7	38.5	38.6	38.7	38.7	38.4
38.2	38.4	38.4	38.2	38.1	38.2	0	0
Jugular temperature (°C)							
38.2	38.3	38	38	38.1	38.1	38.1	38
37.9	38	38	37.8	37.7	37.9	0	0
Ear skin temperature (°C)							
32.5	32.8	27.5	25.5	28.5	32.3	32.8	33.6
19.5	19.1	17.7	22.1	22.6	22.9	0	0
Leg skin temperature (°C)							
20.2	20	19.8	19.2	18.8	18.5	19.4	21.1
17.4	17.8	17.8	18.1	18.6	19.1	0	0
Trunk skin temperature (°C)							
28.1	27.7	27.3	28.8	28.3	28	27.7	27.7
26.1	26.4	26.7	26.9	27.6	27.2	0	0
Rumen core temperature (°C)							
39	38.9	36.4	36.7	37.8	38.7	39.2	39.5
39.4	39.5	37.3	36.1	37.7	38.6	0	0
Oxygen consumption (litres.h ⁻¹)							
1.14	1.08	1.5	1.79	1.5	1.45	1.38	1.4
1.09	1.06	1.51	1.79	1.46	1.32	0	0
FROZEN turnip treatment							
Rectal temperature (°C)							
38.2	38.3	38.1	37.4	37.4	37.6	37.8	38
38.5	38.6	38.3	37.9	37.8	38	0	0
Jugular temperature (°C)							
37.9	37.9	37.4	36.5	36.9	37.2	37.5	37.7
38	38	37.5	36.9	37.1	37.5	0	0
Ear skin temperature (°C)							
26.4	30.4	27.7	23.1	22.8	23.1	22.9	25.5
25.7	26.1	23.8	22.1	23	23.4	0	0
Leg skin temperature (°C)							
22.8	23.7	20.7	20.4	20.8	19.4	18.6	19.4
21	21.8	20.8	19.9	19.6	18.6	0	0
Trunk skin temperature (°C)							
29.5	29.2	28	27.7	27.9	26.9	26.8	26.8
29.1	29.2	28.7	28.6	28.6	29	0	0
Rumen core temperature (°C)							
38.2	38.4	33.5	29.3	32.4	36.3	37.3	38.1
39.2	39.2	34	31.8	33.5	35.9	0	0
Oxygen consumption (litres.h ⁻¹)							
1.16	1.06	1.53	2.61	2.16	1.65	1.4	1.36
1.13	1.13	1.87	2.53	2.04	1.58	0	0

Appendix VI Experiment VIII Energy balance data

Lamb #	Period	Treatment	IE	HW	Gross energy intake	Faecal energy output	Urine energy output	Heat production	Energy retention	Mean metabolic body weight
(MJ.day ⁻¹)										
Lamb 14	I	35	COLD		8.15	2.01	0.42	4.74	-0.05	14.8
	II	110	HOT		23.31	7.07	0.84	9.05	+4.91	15.3
	III	20	DRY		5.08	1.18	0.38	3.66	-0.87	15.6
	IV	80	WARM		16.77	4.43	0.62	7.12	+3.65	14.4
	V	55	COOL		13.88	3.76	0.59	6.14	+1.76	16.3
20	I	110	COOL		24.52	8.59	0.93	8.60	+5.22	14.4
	II	80	COLD		17.32	5.63	1.06	6.96	+3.28	15.3
	III	55	WARM		13.88	3.43	0.64	6.05	+2.37	15.7
	IV	20	HOT		4.96	1.23	0.36	3.52	-0.87	15.6
	V	35	DRY		8.70	1.94	0.47	4.88	-0.21	15.4
38	I	20	WARM		4.61	0.98	0.37	3.70	-1.08	14.1
	II	55	DRY		11.73	2.94	0.67	5.00	+1.26	13.7
	III	110	COLD		23.77	7.23	0.89	8.57	+4.95	14.2
	IV	35	COOL		8.15	2.01	0.42	4.74	-0.05	14.8
	V	80	HOT		18.05	5.30	0.68	7.77	+2.82	15.2
41	I	55	HOT		11.73	2.94	0.64	5.10	+1.76	13.5
	II	35	WARM		7.21	1.77	0.47	3.80	+0.22	13.5
	III	80	COOL		16.77	4.43	0.62	7.12	+3.12	15.8
	IV	110	DRY		23.31	7.51	0.47	9.08	+5.15	15.4
	V	20	COLD		5.26	1.31	0.42	4.20	-1.42	15.7
42	I	80	DRY		17.82	5.30	0.77	7.90	+2.34	14.6
	II	20	COOL		4.61	1.26	0.37	3.89	-1.11	14.4
	III	35	HOT		7.67	1.94	0.47	4.19	+0.08	14.6
	IV	55	COLD		12.07	3.57	0.66	5.73	-0.80	14.6
	V	110	WARM		22.76	8.59	0.90	8.82	+3.85	14.4

Daily heat production (MJ.day⁻¹) Experiment IX

Feed Intake level	20		55		80		110	
	g feed.kg LW ^{0.75} .day ⁻¹		g feed.kg LW ^{0.75} .day ⁻¹		g feed.kg LW ^{0.75} .day ⁻¹		g feed.kg LW ^{0.75} .day ⁻¹	
	38	1	38	1	38	1	38	1
Rumen infusion temperature (°C)	38	1	38	1	38	1	38	1
Lamb 14	4.92	5.43	5.72	5.69	7.49	6.40	8.78	8.07
20	4.07	3.76	5.13	5.14	6.50	6.19	9.10	9.76
38	4.04	5.62	5.03	5.76	5.60	6.73	7.51	7.78
41	4.28	4.62	5.27	5.91	6.56	8.50	-----	8.11

Heat production (W.m⁻²) Experiment X

Ambient temperature (°C)	+8		-8		-20	
	Steer	Hour	Steer	Hour	Steer	Hour
Ration	Horny Polly	1 2	Horny Polly	1 2	Horny Polly	1 2
WARM	93	105	104	93	122	117
TURHAY	85	121	102	104	109	103
COLD	111	113	115	109	120	118
FROZEN	133	120	146	106	169	129

Heat production (W.m⁻²) Experiment XI

Feed intake level	20		35		55		80		110	
	g feed.kg LW ^{0.75} .day ⁻¹		g feed.kg LW ^{0.75} .day ⁻¹		g feed.kg LW ^{0.75} .day ⁻¹		g feed.kg LW ^{0.75} .day ⁻¹		g feed.kg LW ^{0.75} .day ⁻¹	
	38	1	38	1	38	1	38	1	38	1
Ambient temperature (°C)	+10	-20	+10	-20	+10	-20	+10	-20	+10	-20
Lamb 14	47	66	56	73	57	72	61	102	77	51
20	44	70	52	79	51	102	52	115	66	101
38	40	86	59	98	53	99	66	131	57	117
41	51	75	52	40	59	81	66	73	70	64

Appendix VIII

Calculation of heat gained by the rumen during and after rumen cooling, FED and NOT FED treatments (Experiment I)

1. Rumen mass was calculated from the difference in rumen temperature at the end of cooling by the INFUSION and COIL method of rumen cooling (see Experiment I)
2. Total heat gained by the rumen over 3 hours was calculated as the total cooling of the rumen less the residual heat debt in the rumen at the end of the recovery period $((\text{rumen mass} \times (T_{ru\text{initial}} - T_{ru\text{final}})))$
3. The total rumen temperature deficit was calculated over the cooling phase from the mean rumen temperature over 30 min intervals and over the recovery period of hours by the integrated area (at 30 min intervals) of the exponential recovery of rumen temperature
4. In the NOT FED treatment, the total heat gained by the rumen (from (2)) was allocated over 30 min periods according to the total rumen temperature deficit (from (3))
5. Using the relationship of heat flow per °C temperature deficit (from (4)), the heat flow from the body to the rumen in the FED treatment group was calculated
6. The change in heat content of the rumen at 30 min intervals, less the calculated heat flow from the body to the rumen was taken as the heat gained by the rumen from microbial fermentation.

B30294